

Q4
5343
EIT
W-22
76.2

FR
THE UNIVERSITY
OF MICHIGAN
JUN 23 1960
SCIENCE
LIBRARY

ECOLOGICAL MONOGRAPHS

VOL. 30

APRIL, 1960

NO. 2

OFFICIAL PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA

CONTENTS

Changes in Vegetation, Structure, and Growth of South- western Pine Forests Since White Settlement

Charles F. Cooper
(Pp. 129-164)

Aspects of the Ecology of the California Pebble Crabs (Crustacea: Xanthidae)

Jens W. Knudsen
(Pp. 165-185)

Energy Dynamics of a Food Chain of an Old-Field Community

Frank B. Golley
(Pp. 187-206)

Primary Productivity and Limiting Factors in Three Lakes of the Alaska Peninsula

Charles R. Goldman
(Pp. 207-230)

PUBLISHED QUARTERLY BY DUKE UNIVERSITY PRESS
DURHAM, N. C., U. S. A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

EDITORS: BOTANY, H. J. OOSTING, Duke University, Durham, N. C.
ZOOLOGY, FRANCIS C. EVANS, University of Michigan, Ann Arbor, Mich.

BUSINESS MANAGER: WILLIAM G. OWENS, Duke University Press,
College Station, Durham, N. C.

MEMBERS OF THE EDITORIAL BOARD

1958-60

F. H. Bormann, Department of Botany, Dartmouth College, Hanover, N. H.
N. G. Hairston, Department of Zoology, University of Michigan, Ann Arbor, Mich.

1959-61

E. J. Dyksterhuis, U. S. Soil Conservation Service, Lincoln, Nebr.
E. W. Fager, Scripps Institute of Oceanography, La Jolla, Calif.

1959-60

John J. Christian, Penrose Research Laboratory, Philadelphia Zoological Garden,
Philadelphia, Pa.
John Goodlett, Harvard Forest, Petersham, Mass.

EX OFFICIO: Alton A. Lindsey, Purdue University, Lafayette, Ind.
Lamont C. Cole, Cornell University, Ithaca, N. Y.

The editorial board of this journal will consider ecological papers which are in general long enough to make twenty printed pages or more. Shorter ecological papers should be submitted to the editor of *Ecology*, which is also published by the Ecological Society of America. Both journals are open to ecological papers from all fields of biological science.

Manuscripts should be typewritten with ample margins on 8½ x 11 in. paper. A "Table of Contents" should be included. Authors should try to conform in editorial detail in so far as it may be determined from inspection of recent numbers of the journal. Reprints, with or without covers, are obtainable at cost and should be ordered when proof is returned. Correspondence concerning editorial matters should be sent to the appropriate editor; that concerning subscriptions, change of address, and back numbers to the Business Manager, Duke University Press.

Subscription price: the United States, Canada, and the Pan-American Countries, \$6.00 per year; all other countries—\$8.00 a year additional for postage. Single numbers of the current volume are \$1.75. Back numbers, \$3.00 per volume, \$2.00 per number. Missing numbers will be supplied free when lost in the mails if written notice is received by the Circulation Manager within one month of date of issue. All remittances should be made payable to the Duke University Press, Box 6887, College Station, Durham, N. C.

Agents in Great Britain: The Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Prices can be had on application.

Entered as second-class matter December 18, 1930, at the Post Office at Durham, North Carolina, under the Act of Congress of March 3, 1879.

COPYRIGHT, 1960, BY THE DUKE UNIVERSITY PRESS



CHANGES IN VEGETATION, STRUCTURE, AND GROWTH OF SOUTH-WESTERN PINE FORESTS SINCE WHITE SETTLEMENT

CHARLES F. COOPER

Department of Botany, Duke University, Durham, N. C.*

TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	129	Growth and Needle Weight of Individual Trees	147
THE HISTORICAL EVIDENCE	130	Height of Dominants as a Function of Age and Stocking	148
Original Condition of the Pine Forest	130	Pattern	148
Climatic Change	133	Forest Conditions at Maverick and at Malay Gap	150
Grazing	134	Fire in the Ecology of Ponderosa Pine	150
Wildlife	136	Stand Structure at Maverick and at Malay Gap	151
Fire	137	Fire Effects on Sapling Stands	153
The Indian, Fire, and the Forest	138	Mechanism of Thinning by Fire	154
THE EVIDENCE FROM STAND STRUCTURE	138	Early Growth of Present Mature Stand	155
Area of Study	138	Sapling Stands at Maverick and at Malay Gap	156
Age and Size Class Distributions in Old-Growth Stands	139	The Origin of Pattern and Structure	157
Diameter Class Distributions	139	Age and Diameter Structure	157
Age Class Distributions	140	Pattern	158
Structure and Growth of Sapling Stands	142	Ground Cover Vegetation	159
Diameter Class Distributions in Even-Aged Reproduction Stands	142	Effects of Fire on Soils	160
Age Classes of Reproduction Stands	143	DISCUSSION AND CONCLUSIONS	160
Relation of Mean Growth per Tree to Stocking	144	Changes Since White Settlement	160
Total Stem Growth per Acre	145	Implications for Management	160
Dominance, Suppression, and Mortality	145	SUMMARY	161
Growth of Potential Crop Trees	147	LITERATURE CITED	162

INTRODUCTION

More than a century ago, Lt. Edward Beale wrote of northern Arizona: "It is the most beautiful region I ever remember to have seen in any part of the world. A vast forest of gigantic pines, intersected frequently with open glades, sprinkled all over with mountains, meadows, and wide savannahs, and covered with the richest grasses, was traversed by our party for many days." (quoted by Bell, 1870). There are those today who would agree with the lieutenant's conclusions, but the northern Arizona countryside is no longer the same land that Beale saw in 1857. Eighty-five years of white man's use and occupancy have profoundly altered the forest landscape. Northern Arizona is particularly suitable for a study of the dynamics of vegetation change under the influence of the white man and his use of the land. Here these changes have taken place within the lifetime of men still living, and are easier to trace than in longer-settled regions.

As in Beale's day, an almost unbroken band of ponderosa pine forest 25 to 40 mi wide and nearly 300 mi long spreads across central and northern Arizona. With outliers in the higher mountains throughout the state, it constitutes one of the largest pine forests in North America. Of the more than 3,000,000 A of commercial forest land in Arizona,

by far the largest part supports a nearly pure stand of ponderosa pine (*Pinus ponderosa*). (The botanical nomenclature of Kearney & Peebles (1951) is followed throughout.) The pine zone occupies most of the mountain and plateau country above about 6,500 ft. On the higher peaks, above about 8,500 ft, the pine is largely replaced by a mixed forest of Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and other species. Below the pine forest lies a pinon-juniper woodland.

This study of vegetation change was approached on the one hand from the historical viewpoint. Due to the late settlement of the region, Arizona is almost unique in the United States in that reasonably well-planned scientific exploration preceded extensive exploitation. Many early travellers left records of their impressions of the pine forest country. Individually, these early reports are of little value in reconstructing the vegetation of the past century. Cumulatively, however, they build up a fairly clear picture.

The second approach was analysis of stand structure. The present mature forest, with an overstory of trees aged 150 yrs. and more, obviously originated before white settlement. The structure of the mature forest was studied and compared with that of the young forest that will comprise the overstory of the future.

This study was made possible by a National

* Present address: Division of Natural Resources, Humboldt State College, Arcata, California.

Science Foundation Predoctoral Fellowship for the academic years 1956-57 and 1957-58. Field work was supported in part by National Science Foundation Research Grant G-3834. Thanks are due to the Tribal Councils of the San Carlos and White Mountain Apache Tribes for permission to carry out the field work on their tribal lands, and to Superintendent Albert Hawley and his staff at the Fort Apache Agency, Whiteriver, Arizona, for assistance. Much useful information was provided by Paul Buss, Forest Manager, San Carlos Indian Reservation, and LaVon Dunford, Forest Engineer, Southwest Lumber Mills, Inc. Among those who assisted with advice and criticism were R. R. Humphrey and C. W. Ferguson of the University of Arizona, J. E. Fletcher of Agricultural Research Service, and F. X. Schumacher of Duke University. Mrs. Lutie Higley, reference librarian at the University of Arizona Library, was unfailingly helpful in the historical phases of the study. Finally, I wish to acknowledge my special debt to Dr. H. J. Oosting of the Department of Botany, Duke University, and to Mr. Harry Kallander, Forest Manager, Fort Apache Indian Reservation.

THE HISTORICAL EVIDENCE

"... the first dayes we founde no grasse, but worser way of mountaines and badde passages, then we had passed alreadie: and the horses being tired, were greatly molested therewith." In those unflattering terms the first white man to leave a permanent record described his visit to the White Mountains (Letter, Coronado to Mendoza, August 3, 1540. Translated in Hakluyt, 1600:375). Francisco Vasquez Coronado forded the Gila River somewhere below the present town of Safford, and crossed the White Mountains to the Indian town of Zuni. Thus began some three centuries of sporadic visits to the northern Arizona mountains by Spanish adventurers, missionaries, and would-be colonists. The mountain region was occupied by nomadic food-gathering Indians, mostly Apaches and their close relatives, the Navajos. The Spanish conquistadores found that these people could not be conquered by the means then available to Spain, they would not stay converted, and they had no property worth stealing (Webb, 1931). So, "Nearly all of what we now call Arizona has no other history before 1846 than the record of exploring entradas from the south and east" (Baneroff, 1889). A relatively few Apaches, masters of guerilla warfare, were able to prevent white settlement and to hold the country for themselves for more than 300 yrs.

The Treaty of Guadalupe Hidalgo transferred Arizona and New Mexico to American jurisdiction in 1848. Thereafter, the Apaches were an American problem for nearly 40 yrs. Sporadic and confused attempts at control were ended by the Civil War. After the war, serious efforts to subdue the Apaches got under way. More or less permanent peace came to the north and west in 1874, and the northern pine

country was open to settlement and exploitation by white men.

ORIGINAL CONDITION OF THE PINE FOREST

"We came to a glorious forest of lofty pines, through which we have travelled ten miles. The country was beautifully undulating, and although we usually associate the idea of barrenness with the pine regions, it was not so in this instance; every foot being covered with the finest grass, and beautiful broad grassy vales extending in every direction. The forest was perfectly open and unencumbered with brush wood, so that the travelling was excellent." (Beale, 1858). The overwhelming impression that one gets from the older Indians and white pioneers of the Arizona pine region is that the entire forest was once much more open and park-like than it is today. A critical examination of early reports of travellers in northern Arizona at the time of white settlement may shed some light on primeval forest conditions, and on changes in those conditions within historic times.

There are no reliable reports from the northern mountains until after 1848. The first official expedition, under Capt. Lorenzo Sitgreaves, missed most of the forest area. Lt. Whipple in 1853 led a party surveying a possible route for a transcontinental railroad along the 35th parallel. Lt. Beale, commanding the famous band of camels that was expected to revolutionize transportation in the Southwest, crossed the area in 1857 and again in the winter of 1858-59. Lt. Ives explored the Colorado River and led the first expedition into the Grand Canyon country. After the Civil War the number of military and civilian visitors increased rapidly. The period of exploration culminated with the expeditions of the Wheeler Survey, predecessor of the present U. S. Geological Survey, in the years 1871-1875. Accompanying virtually all these early expeditions was a naturalist whose duty it was to describe the country for the benefit of prospective settlers and to collect information on the botany, zoology, and geology of the region.

Most of the early travellers were impressed by the open nature of the forest. Ives (1861) described the region at the base of Bill Williams Mountain: "This morning we re-entered the region of pines, and have travelled all day in the midst of picturesque and charming scenery. The valleys are covered with a bright green sward, and open groves are dispersed gracefully upon the lowlands and ridges." Joseph Rothrock (1875), botanist with the Wheeler Survey, wrote of the region just south of Gallup, New Mexico: "Gaining the summit a thousand feet above Fort Wingate, we were at an altitude of about 8000 feet above the sea, a fine, open, park-like region with a large growth of yellow pine (*Pinus ponderosa*) and fir covering the hillsides. A diversified herbaceous vegetation was out in the most brilliant colors, beautifying alike the woods and open grounds. . . . Good forage was abundant." This area today is almost

bare of herbaceous ground cover, and dense thickets of pine saplings predominate.

The glowing reports of Lt. Beale have already been quoted. Whipple (1856) was more restrained in his comments, but he too remarks on the open nature of the pine forest. C. Hart Merriam (1890) based his life zone concept largely on a study of vertical zonation of vegetation on the San Francisco Mountains. In describing his study area he said, "The lava plateau above about 2130 meters (7000 feet) is covered throughout with a beautiful forest of stately pines (*Pinus ponderosa*) which average at least 33 meters (100 feet) in height. There is no undergrowth to obstruct the view, and after the rainy season the grass beneath the trees is knee-deep in places, but the growth is sparse on account of the rocky nature of the surface." Dutton's classic "Physical Geology of the Grand Cañon Region" (1887) says of the Kaibab Plateau: "The trees are large and noble in aspect and stand widely apart, except in the highest part of the plateau where spruces predominate. Instead of dense thickets where we are shut in by impenetrable foliage, we can look far beyond and see the tree trunks vanishing away like an infinite colonnade. The ground is unobstructed and inviting. There is a constant succession of parks and glades—dreamy avenues of grass and flowers winding between sylvan walls, or spreading out in broad open meadows. From June until September there is a display of wild flowers which is quite beyond description."

Although the early chroniclers were almost unanimous in their description of an open forest, it is evident that some reproduction did exist. Beadle (1873) reported that on the Defiance Plateau, "The tall sugar pines [*sic*] from three inches to two feet in diameter, mingled with a few dwarfish oaks, were scattered in regular proportion." In a report on the Gila River Forest Reserve, Rixon (1905) stated, "The south side of Spring Creek is covered with a phenomenal growth of young pine, approximating 30 feet in height and 6 inches in diameter." In his township by township description of the Reserve, he referred to abundant growth of young pines in some areas, while elsewhere it is not mentioned or is remarked as absent. Plummer (1904), in a similar examination of the Black Mesa Forest Reserve, found exceptionally heavy stands of young trees in some places. Lieberg *et al.* (1904) were struck by the lack of reproduction on the San Francisco Mountain Forest Reserve: "Apparently there has been an almost complete cessation of reproduction over very large areas during the past twenty or twenty-five years, and there is no evidence that previous to that time it was at any period very exuberant." Pearson (1910) early in his career noted that reproduction was generally deficient both in the virgin forest and after logging. He noted, however, that reproduction on the Prescott National Forest was good and in places so dense it was difficult to walk through.

The early explorers were particularly conscious of

grass, upon which they depended to feed their horses. Both Whipple (1856) and Beale (1858) commented about the abundance of grass in the forested area, but both observed that grass was more plentiful on lava soils than on heavier soils derived from sedimentary rocks. Lt. George Wheeler in 1873 was the first white man to climb Mt. Baldy (Mt. Thomas), the highest peak in the White Mountains. He reported that "... a plateau bearing patches of bunch grass is reached. . . . The animals feast upon the rank and succulent mountain bunch grass." (Wheeler, 1878). This would imply that good grass was not universal in the mountains at that time. The same conclusion can be drawn from the reports of Coronado's journey more than three centuries earlier. Coronado (Winship, 1899) spoke feelingly of the difficulty of crossing the White Mountains, and of the good grass at Zuni, "of which we had great need, because our horses were so weak and feeble when they arrived."

Rothrock (1878) described a dense grass cover in the pine zone of southern Colorado: "In the beautiful valley of the Conejos River, after striking the timbered region, we found luxuriant bunch-grass covering the ground as thickly as it could stand. In November it was still green about the roots, and was eagerly eaten by our starved mules. *Pinus ponderosa* formed open clumps, and under protection of these trees it attained what seemed to be its maximum growth." Nelson (1884), a zoologist collecting for the Smithsonian Institution, said of the region above Springerville: "There is scarcely any undergrowth, but a dense mat of grass and flowers in these forests, and beautiful mountain parks are found at frequent intervals."

In the University of Arizona Library is a collection of reports on range conditions in the first decade of this century. Although these reports bear no signature, there can be little doubt that they were written by Dr. J. J. Thornber, Botanist at the Arizona Agricultural Experiment Station. In July, 1905, he travelled by wagon from San Carlos to Fort Apache, across the Natanes Plateau. Thornber (1905) described the Natanes Plateau, which in many places has almost no herbaceous vegetation beneath the pines today, as follows: "The region is one for the most part ungrazed, the bunches of grass maturing large quantities of seed and then dying down to the ground again, thus forming a good surface covering. Also the more or less continuous forest covering contributes considerable in the way of protection for the grasses, so that effects of excessive drought and heat are modified. With the above conditions, it would hardly be too much, except in the densely shaded portions, to expect a continuous turf or sod, but such is the case only for small areas. Most if not all of the grasses are of the xerophytic bunch-grass type; these bunches usually occur at intervals of a few inches to a few feet. They are apparently as abundant on one slope as another. Between these bunches of grass are interspersed many annual and

perennial species, so that there is quite a continuous vegetative covering everywhere over the mountains. In addition to the forest layer, already noted, and the layer of herbs and grasses, there is a fairly well-defined shrub and undershrub layer; in ordinarily closely browsed foot hills and mountains many of these shrubs are considerably browsed by cattle, but so far as could be seen none of these have been nibbled in the least. . . . The region also showed no sign of erosion or gulying, except perhaps where dug away by the hand of man, as along the road." Further on, as he travelled from Fort Apache toward the town of Pinetop, he noted, "There is a thin layer of perennial grasses, covering most of the land from Cooley's to Fort Apache, although it rarely approaches a turf. At this time there is good grazing, but few or no cattle."

At the time of Thorner's visit such good range conditions could probably have been found only on the Indian reservations. More typical were the conditions that Plummer (1904) found on the Black Mesa Forest Reserve. Here forage grasses grew luxuriantly, but only at a distance from water. Carcasses of cattle and horses showed where they had died of thirst after getting too far from water in search of pasture. Beaver Creek, a tributary of the Verde River, was cited as an example of overstocking, resulting in the "complete annihilation of pasture in a formerly rich area."

Deterioration of watershed condition began comparatively early. Bryan (1925) stated that the Rio de Flag, a small creek flowing through a grassy flood plain in the pine region near Flagstaff, had entrenched itself in an arroyo 10 to 20 ft deep. He dated this trenching from 1890 to 1892. That gullies originally were rare in the forest area can be inferred from Dutton's (1887) comments about the Kaibab Plateau: ". . . every ravine is as smooth as a lawn and carpeted with a rich turf of mountain grass, richly decked with flowers of rare beauty and luxuriance."

Pattie (1905) camped on the Gila River in 1826, apparently not far below Gila Hot Springs. He said, "I began to ascend the bank of the stream to explore. . . . The first day we were fatigued by the difficulty of getting through the high grass, which covered the heavily timbered bottom." There is little grass in the eroded Gila Canyon today. Leopold (1921) said of Blue River, a tributary of the upper Gila, "All the old settlers agree that the bottoms of Blue River were, at the time of settlement in about 1885, stirrup-high in gramma grass, and covered with groves of mixed hardwoods and pine. The banks were lined with willows and abundant with trout. . . . About 1900, fifteen years after settlement, floods began to cut an ever-widening channel."

Wheeler (1878) stated that in the White Mountains, "Elk, mountain sheep, California lion, deer, antelope, wild turkey are known to be abundant in this range, and their fresh tracks were constantly seen." But game was not always plentiful. Nelson (1884) wrote that ". . . the twentieth of August found

us located at Springerville. . . . Although the mountains about here have been noted for the abundance of game in them during past years, yet all kinds of large game were remarkably scarce during the past season. . . . Bear were not to be found at all, and elk were so scarce that only a single fresh track was seen during several weeks in the woods. Although the cattlemen have invaded the district in force, yet they have only touched the pine country at widely scattered places, and I am unable to account for the scarcity of large game." At about the same time, Frazier (1884) visited the Apache Reservation on behalf of the Indian Rights Association. He reported that "Game is scarce on the reservation, and the Indians find it difficult to find animal food." Even earlier, Indian Commissioner Dole noted a shortage of game at the time of the Civil War (Ogle 1940). Thus it appears that big game was by turns abundant and locally scarce even before white men had much influence on the region.

The most notable game animal in Arizona was the Merriam elk, now extinct. Its principal range was the White Mountains, but it occurred throughout Arizona and New Mexico. It was reported around Flagstaff as late as 1884, and apparently persisted in isolated areas until the early years of the present century. Rocky Mountain elk have since been transplanted to Arizona.

The history of deer in Arizona has been one of alternating scarcity and overabundance. In most of the mountain areas of the state deer have thrived in recent years and are probably at least as numerous as they have ever been. No really radical changes have been noted in the abundance of most of the other conspicuous forest animals—wild turkeys, squirrels, and others. An intensive predator control program has eliminated the grizzly bear and the wolf, and considerably reduced the numbers of bear, coyotes, and mountain lion.

Changes in the Arizona pine forests were summarized more than 50 yrs ago by Holsinger (1902), an examiner for the General Land Office: "Briefly, the history of the forests of Arizona, which my opportunities have enabled me to gather from many of the oldest reliable pioneers, is that when first invaded by white man the forests were open, devoid of undergrowth, and consisted in the main of mature trees, with practically no forest cover. Instead of forest undergrowth, the ground was well set with perennial grasses and other herbage, which, being undisturbed, maintained what may be called a normal condition, or such as existed when the country was first settled and such as is now much to be desired. It was not an uncommon thing for the early settlers to cut native hay in the pine forests and fill large government contracts at the different military posts. As an instance, Fort Whipple, near what is now the Prescott forest reserve, may be mentioned. Where hundreds of tons of hay were cut under the actual spread of the forest trees during the sixties and seventies, there is not now enough grass on a thousand acres to keep in condition a family cow. Where were then running

streams are now dry arroyos, and where were then living springs are now beds of silt and sand."

An examination of the record tends to substantiate Holsinger's conclusions. The forest was decidedly open and parklike. Reproduction was present but not abundant, and in many areas was markedly deficient. Grass was abundant, but not universal. Wildlife was probably little if any more plentiful than today, although some species such as the grizzly bear and the lobo wolf have long since disappeared from the state.

The most conspicuous change that has taken place in most parts of the region is the increase in area and density of pine reproduction stands (Fig. 1). Few parts of the southwestern pine region today lack young trees. Grass density has been greatly reduced, and in some places ground cover vegetation is virtually absent (Fig. 2). A combination of factors, operating over the past 75 yrs, has brought these changes about.



FIG. 1. A typical thicket of 38-yr-old ponderosa pine. In the densest portion of this stand, there are the equivalent of 10,000 stems per A or more.

CLIMATIC CHANGE

To evaluate the importance of climatic change, it is necessary to consider how climate affects the growth and reproduction of ponderosa pine. Moisture is the critical factor regulating the distribution of this species, and a severe dry period in the spring of the year hinders regeneration. In the Southwest, a peculiar combination of weather conditions must occur before seedlings can become established.

According to Maguire (1956), whenever average monthly temperatures during April and May are considerably above normal, ponderosa pine will flower in abundance the following spring, with resulting large cone crops in the fall of the next succeeding year. In the Southwest, good cone crops occur about once every 3 or 4 yrs, with a real bumper crop at irregular intervals (Pearson 1950:111). Establishment of a reproduction stand requires coincidence of a good seed crop and favorable growing conditions during the year or two after germination. Seeds commonly germinate in July and August, during the summer rains. If the rains are closely spaced, incredible numbers of seedlings sometimes germinate.



FIG. 2. A dense cover of mountain muhly (*Muhlenbergia montana*) is characteristic of moderately grazed pastures such as the one on the right. Overgrazing has eliminated virtually all herbaceous vegetation on the left side of the fence.

For instance, in September, 1957, as many as 30 to 40 seedlings per square foot could be counted in parts of the White Mountains. In a normal dry spring, no seedlings of the previous summer's crop will live. Only in an unusually wet spring can stand establishment be expected.

A peculiar combination of weather conditions, then, is needed to establish reproduction: a warm spring in one year, resulting in a heavy seed crop 27 months later. The summer and autumn after seed fall must be wet, and the following spring must also be wetter than normal. Such a combination of events in a semi-arid region can be considered a climatic accident, rather than a part of the normal weather pattern.

The available weather data from Arizona are of limited use in assessing long-term climatic change because of the shortness of the record. There was a severe drought in the last decade of the nineteenth century, a wet period from about 1904 to 1930, and a renewed drought since that time. The drought of the 1890's had a marked effect on the grazing history of the region, and was apparently severe enough to kill pine trees near the lower forest border. Plummer (1904) reported that trees were killed by drought in the vicinity of Heber and near Blue. There is no evidence, however, of a recent major change in climate.

One of the most publicized sources of long-term climatic data is analysis of tree rings. Tree ring

studies in the Southwest have been carefully analyzed by Schulman (1956). He showed that an irregular alternation of wet and dry periods has been characteristic of the entire period of the existing tree ring record. In the Gila River basin, analyses of more than 100 trees show that there were marked dry periods in the years 1800-1825, 1841-1847, 1861-1864, 1871-1904, and 1921-1953. Wetter than usual periods were characteristic of the years 1826-1840, 1848-1860, 1865-1870, and 1905-1920. His general index for the entire Colorado River basin, which extends the record further back in time, shows similar irregular fluctuations for about 900 yrs back from the present. On the basis of tree-ring chronologies, Schulman (1956:67) stated that the current drought in the Gila River basin is the most severe since the late 1200's. This drought is interpreted as having begun in 1921 in some parts of the basin, in 1934 in others.

Schulman pointed out, however, that his analysis is based on ring widths measured as a percentage departure from a moving mean. Small secular changes in climate may be completely hidden by this moving mean procedure. Short-term departures (droughts and wet periods) from the mean are easily detectable, but longer-term changes in overall climate would not be evident from tree ring data.

Hack (1942) studied the evidence for long-term changes in the environment of the Hopi Indians, whose home is some 80 mi north of the forest area. He concluded from the stratigraphy of stabilized and active dunes that the climate was much drier than at present during the period from about 5000 to 2000 B.C., and that the climate of the first millennium A.D. was apparently moister than it is today. Stratigraphy of alluvial sediments in arroyo banks pointed to a similar conclusion, with a minor wet period between 1300 and 1700 A.D. Antevs (1955) concluded from geologic and archeologic evidence that there was a warm peak about 3000 yrs ago, followed by a rather abrupt decline to the general temperature of the present. There were severe droughts about 500 B.C. and 330 A.D., and during the years 1276-1299 and 1573-1593. Other comparable periods in the past thousand years have been somewhat wetter than the present.

On the basis of the rather scanty evidence available, there seems to be no reason to believe that there has been a large-scale climatic change in the past 1000 yrs of a type that would profoundly modify the character of the pine forest. Certainly there have been minor fluctuations, from relatively wet to relatively dry. The recent drought began about 1930, whereas the current overabundance of reproduction dates from at least a decade earlier.

The question of climatic accidents is less easily disposed of. There is no way to determine from the historical record how frequently the peculiar combination of events necessary to initiate extensive pine reproduction could have occurred in the past. The great spatial and temporal variability of precipitation described by McDonald (1956) makes it appear that

such a combination is entirely a chance occurrence. Perhaps the 1919 reproduction year of which Pearson made so much was a highly improbable situation that could be expected to recur only once in several centuries. If so, the present condition of the pine forest might be ascribed in large part to this single climatic accident. It seems likely, though, that similar accidents have occurred since time immemorial. Climatic change, either in the form of long term trends or of an unusual combination of weather conditions in one period of years, does not appear to offer a satisfactory explanation of changes in the pine forest.

GRAZING

The overuse and mismanagement which followed introduction of livestock into the West produced profound changes, some of them permanent, in the plant cover. Because these changes were conspicuous and well publicized, the stockman has been blamed for many of the ills of forest land management. In particular, overgrazing has often been assigned as the primary cause of the overabundance of young pines.

Utilization of the ranges of northern Arizona did not begin to any great extent until the late 1870's. Within a few years after the subjugation of the Indians the ranges began to fill up. The Navajo country, including the pine area on the Defiance Plateau, was heavily grazed for years before that time, however. Charles Bent (1851), in a letter written during the Mexican War estimated that the Navajos possessed 30,000 cattle, 500,000 sheep, and 10,000 horses, mules, and asses. These figures seem a little high, but that the Navajos owned extensive herds is attested to by Lt. Simpson (1850), who wrote from Canyon de Chelly: "Innumerable signs of stock, principally sheep, have been seen along the route, and the road we have been travelling looks as if it might be one of the great thoroughfares of the nation." Unlike the Navajos, the Apaches kept no stock, preferring to steal animals that their neighbors had raised.

Sheep preceded cattle into most of the Arizona mountains. Heavy settlement of northeastern Arizona began about 1876, and few good locations remained unoccupied by 1880. Sheep outnumbered cattle by 10 to 1 at this time (Haskett, 1936). As cattle began to replace sheep, the mountains were used primarily by stockmen who had their headquarters in the shortgrass plains at lower elevations.

Social and economic conditions at that time were such as to prohibit conservative and intelligent management of the range, even had the requisite knowledge been available. Cattle prices were too low to permit ranchers to do much more than turn their cattle loose and gather the increase at periodic intervals. Virtually all the range was vacant and uncontrolled public land. While each outfit had its own "accustomed range" which was generally recognized, that range had to be occupied or someone else would move his stock in. Thus it became a race to place cattle on the summer ranges as soon as a spear of grass appeared, for fear of losing out altogether.

Under such conditions abuse and deterioration of the range was inevitable.

By 1889 Farish (1889) could write of the San Francisco Mountains: "In this mountain range are found fine valleys, formerly covered with a growth of wild rye and pea vine, which has been replaced by other grasses." Replacement of the better forage plants had taken no more than a dozen years after the introduction of livestock. In 1892 a severe drought combined with range depletion to cause heavy stock losses, which became even worse in 1893. The Governor of Arizona stated in his annual report: "In nearly all districts, owing to overstocking, many weeds have taken the place of the best grasses. In other places where ten years ago the end of the wet season would find a rich growth of grass, now it is of inferior quality, or less quantity, or does not exist at all." (Hughes 1893).

Conditions were probably at their worst by the turn of the century. Serious concern began to be felt about the influence of overgrazing on water supply. The water problem in relation to forests and forest grazing was made the basis of recommendations for government action in almost every report of the Territorial governors from 1893 to 1910. In the summer of 1910, Sam F. Webb, a representative of the Salt River Valley Water Supply Protective Association, toured the mountains with Gifford Pinchot. His report (Webb 1900) gives a good idea of range conditions in the forest at that time. Speaking of Phoenix Park, between the Mogollon Rim and the town of Pinedale, he says, "Phoenix Park, which once claimed the distinction of being the best and finest portion of that part of the reserve, when we were there, had no running water. Its valley had been ruined by a deep cut or wash draining it so as to render it uninhabited." This is still true today.

At about the same time, Plummer (1904), writing of the present Apache National Forest, reported, "The entire reserve is a natural range, and grazing has been the main industry in this and adjacent regions. In recent years this industry has suffered greatly owing to the continued droughts, and the only remaining areas which are used solely for cattle range are on the Blue and Salt Rivers and Eagle Creek. The Double Circle Ranch, which used to graze over 100,000 head, has been compelled to gradually decrease its herd, until it now numbers not more than 9000. Range for this herd is very limited, and large areas are now being rented from the Apache Indians in the White Mountain Indian Reservation."

As this last statement implies, conditions were somewhat better on the Apache Reservation. Webb (1900) stated, "The White Mountain Indian Reserve was visited and the parks in it showed no deep cuts or channels to carry the rain water away in torrents." Webb attributed this difference entirely to differences in grazing use. He did not appreciate that the soil of Phoenix Park is highly erodible when disturbed, while the basalt soils of the Indian Reservation are much less susceptible to erosion (Fletcher & Beutner 1941).

There is apparently less grass in most of the mountains of Arizona today than there was at the coming of the white man. Two factors have tended to reduce forage production on pine bunchgrass ranges (Arnold 1950). Under heavy grazing the original tall bunchgrasses have been largely replaced by plants more resistant to grazing, except where dense tree cover discourages livestock use. In addition, grass cover decreases as pine reproduction becomes established; the greater the density of pine saplings, the less the total herbaceous cover. Decline in total forage production as a result of competition from young pine stands is accompanied by no great botanical change in the herbaceous vegetation, but heavy grazing induces a major change in species composition. In openings within the forest, ranges in good to excellent condition near Flagstaff support a high proportion of midgrasses, dominated by Arizona fescue, mountain muhly, muttongrass, and June grass. Under heavy grazing pressure, the midgrasses are replaced by a shortgrass cover composed largely of blue grama and squirreltail. Under still more severe use, even these resistant grasses are largely replaced by less desirable perennial and annual forbs (Arnold 1955).

The adverse effects of overgrazing on soil and water movement have been described so often that little repetition is needed here. Arnold (1955) reported that of the mountain meadows examined in northern Arizona, those in excellent condition showed no gullies. Two of the 13 meadows classed as good had gullies, but these were less than 2 ft deep. The degree of gullying increased to the point that of 14 meadows in very poor conditions, 10 had deep gullies and 2 had shallow gullies. Degree of gullying, however, is in considerable degree dependent on the erodibility of the soil. Fletcher & Beutner (1941) showed that basalt soils were far less erodible than soils supporting a similar vegetation but derived from sedimentary rocks or granite. This is apparent in the White Mountains, where severe gullies rarely develop in the basalt soils, even under heavy range abuse, although soils derived from other rock types are often badly eroded.

Browsing by livestock has had a direct effect on pine reproduction, particularly in the early days of heavy grazing. Pearson (1950:157) discussed in some detail the relation of regeneration to browsing animals. Sheep eat both growing shoots and needles, while cattle normally eat only shoots. This difference in feeding habits, plus the heavy grazing that results from the close herding of sheep, makes sheep more damaging than cattle. In the early years of this century, many areas were completely denuded by sheep. Webb (1900) reported that south of Springerville, "From 1875 to 1882 Tranquilino Luna is reported to have had sixty thousand sheep grazing annually on the Gila Forest reserve, and made Luna and one or two neighboring localities his lambing grounds. Since that date but little stock has roamed over the region. When we were there no grass or anything in the shape of feed except a few scattering

weeds could be seen. The grass roots and seeds have been destroyed. No young pines of over fifteen years growth were observed." Lieberg *et al.* (1904) also reported wholesale destruction of small pines by sheep on the San Francisco Mountain Forest Reserve.

The large reduction in numbers of livestock permitted on national forests, plus the extensive conversion of sheep operations to cattle, have greatly alleviated the browsing problem. Localized damage continues due to livestock concentration, but is relatively minor. The results of past browsing damage, however, are clearly apparent in large areas that lack reproduction due to past sheep use.

Grazing has been important in reducing the spread of fire. Large amounts of inflammable grass, which used to remain on the ground, are now removed by grazing animals. Many of the early arguments against reduction of grazing on the national forests were based on the premise that heavy grazing made forest fires much less frequent.

It has been widely held that removal of herbaceous cover and plant litter by grazing animals, and the exposure of mineral seedbeds by livestock trampling have been important factors in the establishment of dense pine stands. Pine seeds germinate well under proper weather conditions on almost any type of ground cover, but they soon die from desiccation unless they become rooted in mineral soil. In addition, direct root competition for soil water from the established grass cover is considered to inhibit seedling growth. Rummel (1951) compared Meek's Table, an ungrazed mesa in central Washington, with Devil's Table, a grazed mesa supporting a dense stand of young ponderosa pine. He concluded that herbaceous vegetation as dense as that found on Meek's Table definitely inhibited establishment of ponderosa pine reproduction. His study did not indicate the critical density of ground cover vegetation which would permit the establishment of either adequate or overabundant reproduction. His discussion clearly implies, however, that there is an almost straight-line relationship between degree of reduction of the virgin herbaceous stratum and quantity of pine reproduction. He concluded that heavy grazing is the primary factor which accounts for the dense reproduction on Devil's Table.

In contrast, a much earlier study by Pearson (1923) in Arizona showed that "competition with grasses is less disastrous to yellow pine seedlings than might be expected." Although grass competition slowed seedling growth, stand regeneration proceeded even in the presence of a grass cover. Seedlings were severely handicapped in the densest grass areas, but even here a few were able to establish themselves.

Nearly 20 yrs later, Pearson (1942) confirmed earlier findings that dense herbaceous vegetation retards pine reproduction. Grass and other herbaceous plants are able to appropriate most of the moisture in the upper nine inches of soil at the expense of pine seedlings. Until they have developed a deep root

system, grass competition puts the young pines at a disadvantage.

Lavin & Springfield (1955) planted ponderosa pine seed in a 2-yr-old artificially planted stand of herbaceous vegetation, of several species and densities. At the end of the second season, seedling survival was inversely related to the total coverage of the herbaceous plants, but the decrease in survival was only moderate as competition increased. They concluded that, "Although herbaceous vegetation, seeded and native alike, adversely affects pine seedling survival, fairly good survival was obtained in spite of this competition." Of course, the density of the reseeded grasses did not approach that of the natural vegetation that Rummel found on Meek's Table.

These studies show that ground cover vegetation strongly affects growth and survival of pine seedlings. Most of the studies cited do not devote enough attention to the unusual weather conditions required for pine reproduction. In a normal year, most if not all pine seedlings in a virgin forest will die regardless of competition. In the rare year in which a wave of seedlings establishes itself, there may be so much moisture that no degree of herbaceous competition is really inhibitory. Reduction of competition may be a means of encouraging better reproduction in managed stands, but under virgin conditions it appears that seedlings could have developed even in a heavy grass cover. The reduction of grass competition and the preparation of a mineral seedbed by grazing animals probably helped to bring about the dense thickets, but do not seem to have been the controlling factor. There are many severely grazed openings which remain nearly denuded of vegetation and in which pine seedlings have not become established.

WILDLIFE

The relation of deer to the ponderosa pine forest has long been a matter of concern. The Kaibab deer herd has profoundly modified the vegetation of its range (Rasmussen 1941). As a result of removal of natural predators and of restriction of hunting, this herd built up from an estimated 4000 deer in 1906 to nearly 100,000 in 1924. By that time the range was depleted, there were deaths by the thousand from malnutrition, and the population dropped precipitously. Parts of the pine area were so severely browsed that reproduction was eliminated.

Elsewhere the deer problem has not been so acute. Pearson (1950) stated that deer eat pine buds early in spring when elongation begins, and occasionally they will take shoots that are distinctly woody. Deer tend to concentrate where use by livestock is light. On the whole, deer have probably played a relatively small part in recent changes in the pine forest. Heavy hunting pressure greatly reduced deer populations in most of Arizona, except the Kaibab Plateau, during the early years of this century, and only recently has the deer herd built up to its present level. Elk, never very common, were quickly exterminated,

and the introduced elk are not numerous enough to have more than a local effect on vegetation. Obvious browsing by elk was noted in the upper branches of small pines after they were cut on experimental plots near Maverick in November, 1957.

Rodents and other small mammals were considered very important by Pearson (1950:151). He was concerned about the use of seeds by mammals, the girdling or complete cutting of seedlings, and the removal of bark from larger trees. Taylor & Gorsuch (1932) found that birds, ground squirrels, chipmunks, and mice all ate pine seeds. They concluded, though, that under natural conditions seed-eating rodents have little or no detrimental effect on reproduction of ponderosa pine. When favorable conditions occur, seedlings develop in spite of all obstacles.

Keith (1956) made a thorough study of the Abert squirrel, which Pearson classed as one of the most damaging of animal agents. Keith concluded that the squirrel is well adjusted to the climax forest, and that it has very little real effect on the forest as a whole. There is little basis for assuming that wild animals have been more than a minor factor in inducing changes in the pine forest in historic times.

FIRE

The principal assignment of the early foresters in the Southwest was the exclusion of fire from the woods. They recognized that fires had been frequent, and that a surface fire could pass through a ponderosa pine forest without destroying it, but each such fire was considered another step contributing to final destruction. John Wesley Powell (1879) believed that "The protection of the forests of the entire Arid Region of the United States is reduced to one single problem—Can the forests be saved from fire?"

Reporting on the newly formed San Francisco Mountain Forest Reserve, Lieberg *et al.* (1904) wrote: "It is very evident that the yellow pine stands, even when entirely untouched by the ax, do not carry an average crop of more than 40 per cent. of the timber they are capable of producing. . . . These conditions are chiefly attributable to the numerous fires which have swept over the region within the last two hundred years, carrying with them the inevitable consequences of suppression and destruction of seedling and sapling growth."

There is little doubt that fires, started by lightning or by Indians, were frequent in the pine forest before the arrival of the white man and in the early years of settlement. Weaver (1951a) analyzed the fire scars on stump sections collected at various sites in Arizona. The most frequently burned tree showed an average interval of 4.8 yrs between fires, while the longest average interval between fires exhibited by any sample tree was 11.9 yrs. Weaver's data are borne out by the results Show & Kotok (1924) obtained in California. They found that during the 200 yrs for which the tree ring record is fairly complete, 25 clearly marked fires were detectable. The average fire frequency of about 8 yrs held true for all Cali-

fornia areas studied. The shortest interval between fires was 3 yrs and the longest 11 yrs.

Early visitors to the Southwest apparently took for granted the frequency of surface fires in the pine forest. Wheeler (1878) was a few miles north of Black River on August 27, 1873, when he wrote, "Here, as has been noticed in several other localities, the grass on one side of a stream will be new, juicy, and thin, because of the burning of the sward during the season, while on the opposite side, where no burning has taken place, the thick tufts of bunch grass spreading into beds offer more abundant feed for the animals that now have to depend upon grass altogether for their support."

Despite the frequency of surface fires, serious crown fires were apparently rare. A fairly thorough search of the early literature failed to turn up a single report of a crown fire in Arizona before 1900. A Forest Service report (Drake 1910) on the Cocino National Forest stated that over 80% of the yellow pine type had been burned over one or more times, but that the fires usually destroyed only a small amount of standing timber. Only two burns were noted which destroyed the stand: one of 7000 A in spruce about 30 yrs previously, and the other of 3200 A in juniper woodland near Winona. With the possible exception of a part of the Prescott National Forest, there appears to be no area in Arizona where extensive even-aged pole stands indicate that a major fire destroyed most of the mature timber and permitted extensive even-aged regeneration. There is no evidence elsewhere of fires of the magnitude of the Escudilla fire of July, 1951, which destroyed most of the timber on 19,000 A, or the 21,000 A Dudley Lake fire of June, 1956.

The situation in California ponderosa pine was evidently similar to that in the Southwest. Sudworth (1897), reporting on the Stanislaus and Lake Tahoe Forest Reserve, said, "The fires of today are peculiarly of a surface nature, and there is no reason to believe that any other type of fire has occurred here. . . . The instances where large timber has been killed outright by surface fires are comparatively rare. Two cases only were found. . . . One of these burns involved less than an acre, and the other included several hundred acres. They are exceptional cases, and the killing of the trees is accounted for by the fact that protection from fire and from all but cattle grazing has resulted in the accumulation of much fallen timber, considerable humus in depressions and on benches, and a dense undergrowth of brush and seedlings."

The occurrence of forest fires far back into antiquity was noted by Holsinger (1902). In Chaco Canyon, New Mexico, he found that where a deep arroyo had cut to a depth of 30 ft through a sedimentary formation, distinct strata of earth, impregnated with charcoal, lay about 15 to 20 ft from the surface and could be traced over an area of several thousand acres.

Opinions of early foresters about fire in ponderosa pine were summarized in the detailed study of Show

& Kotok (1924) on the role of fire in the pine forests of California. They concluded that "The present California pine forests represent patchy, understocked stands worn down by the attrition of repeated light fires. . . . Each successive fire adds its often imperceptible weight to the force of attrition that thins the stand, weeds out the finest individual trees, and gradually reduces the forest in quantity and quality to the point where the returns will not justify the cost of logging." They reported that each fire burned down a portion of the mature stand by enlargement of old fire scars, reduced growth rates by physically injuring the trees, and rendered them more susceptible to attack by insects and disease. Young growth suffered most severely from fire. The most conspicuous result of 20 yrs of fire protection in California was "the enormous number of young forest trees that have appeared as individuals or as groups, or in the more virgin stand as a veritable blanket under the mature timber." They concluded that a small amount of reproduction, patchily distributed, is able to survive ground fires, but most of the young stand is inevitably wiped out. In consequence, they felt that fire exclusion would permit nature "to utilize the full growing power of the land, and to restore the broken and understocked forest to a more normal condition."

Dissenting views were heard even in those days. The Annual Report of the Secretary of Agriculture for 1910 said that "The proposal has been made that the Forests should be burned over every year or two in order to prevent the accumulation of vegetable litter on the ground. It has been alleged that the fires which were set in the early days by the Indians and the first settlers were beneficial. As a matter of fact, these early fires were enormously destructive." (U.S. Dept. Agr. 1910). This proposal was dismissed out of hand with the statement, "It is inconceivable that there should be seriously advocated a treatment of the forest that would inevitably result in the very rapid diminution of its density to the point where ultimately there would be no timber at all."

THE INDIAN, FIRE, AND THE FOREST

There is abundant evidence that Indians were responsible for many fires. Stevenson (1881) stated that Indians set fire to the timber on the mountain ranges of New Mexico each fall in order to drive deer down into the canyons. John Wesley Powell (1879) stated that Indians systematically set fire to the forest for the purpose of driving game. The early pioneers of Kanab, Utah, saw great clouds of smoke rolling over the Kaibab Plateau almost continuously from late spring to early fall. Indians were still killing white men in those days, so few trips were made to observe the fires. It was said that Indians chased deer and other game out on the points overlooking the Grand Canyon and then set fires behind them to concentrate game on the very tips (McHenry 1935). On his return from the first ascent of Mt. Baldy, Wheeler (1878) reported that on the higher reaches of the Little Colorado, "For a little less than 2 miles

the grass is of the old crop, then begins the new and juicy growth of the year subsequent to the burning over by fires set by Indians."

Indians had many reasons for setting fires. "The most potent and powerful weapon in the hands of these aborigines was the firebrand. It was used alike to capture the deer, the elk, and the antelope, and to vanquish the enemy. It cleared the mountain trail and destroyed the cover in which their quarry took refuge." (Holsinger 1902). According to Bell (1870), "The Apaches also have a very destructive habit amongst their long catalogue of vices of firing the forests of their enemies." On his trip through the Indian reservation, Webb (1900) found fires burning in two places, which he said were "attributable to the Indians who believe fire and smoke bring rain."

Holsinger (1902) was convinced that "These prehistoric aborigines must have exerted a marked influence upon the vegetation of the country. Their fires, and those of the historic races, unquestionably account for the open condition of the forest, to which reference has been made. The high pine forests were their hunting grounds, and the vast areas of foothills and plateaus, covered with nut-bearing pines, their harvest fields. . . . In Arizona you will find no young forests of any considerable extent antedating a period of forty years, and almost all of the regrowth has sprung up within the last quarter of a century. A single exception can be noted in the White Mountains, which have been occupied for a couple of centuries by the Apache Indians. These forests show, in certain localities, all classes of regrowth, and are in marked contrast to the mountain country occupied by the Navajo Indians in the north-eastern portion of the Territory. The Navajoes have possessed sheep and goats and followed pastoral pursuits for over two centuries. The forest occupied by them shows practically no regrowth. The Apaches have followed the chase and war, and have entrained themselves with nothing but war ponies. The forests within their domain, where they have not seen fit to apply the torch in accord with their well-grounded superstition that forest fires cause rain, show a regrowth gradating into many past decades."

THE EVIDENCE FROM STAND STRUCTURE

AREA OF STUDY

Field work was completed in the summer and fall of 1957, principally on the Fort Apache and San Carlos Indian Reservations. These two reservations lie in east central Arizona, the Fort Apache to the north and the San Carlos to the south of Black River. The ponderosa pine forests of the reservations total about 700,000 acres, mostly on the Fort Apache.

The study area lies in the White Mountains, which form the eastern end of the Mogollon Plateau. East of about longitude 110° and south of the steep escarpment of the Mogollon Rim, the plateau is thickly mantled by Tertiary igneous rocks extruded from the extinct volcanoes that form the heart of the White Mountains. Lava flows, probably of Quater-

nary age, are superimposed on the older topography in the valley of White River and elsewhere (Darton 1925).

The topography of this great lava flow is relatively gentle for a mountain region. Although it is dissected by many steep-walled canyons, its general aspect is that of a gently rolling plateau. The two major peaks of the White Mountains, Mount Ord and Mount Baldy, reach elevations of 10,800 ft and 11,500 ft respectively, but most of the plateau lies below 9500 ft.

The basalt lava which overlies most of the White Mountains is relatively uniform in its composition, as are the resultant soils. One reason for choosing the White Mountains as a study area is the uniformity of its geologic origin, which largely eliminates the influence of differences in parent material on soil development and on plant growth.

Intensive field sampling was concentrated in three areas. The first of these was the old-growth forest about 10 mi west of Maverick, on the east side of Odart Mountain. Studies of reproduction stands were made along Bog Creek, east of McNary, in an area selectively logged in the 1930's. These two locations are about 40 mi apart airline, at an elevation of about 8,000 ft. Soils, climate, and topography are closely similar at both locations, and both are in the heart of some of the best pine forest in Arizona.

The third sampling area was the relatively untouched primitive area around Malay Gap, in the extreme northeast corner of the San Carlos Indian Reservation. This is perhaps the closest approach to a truly primeval forest left in the Southwest. Until the last few years there has been no usable stock water in the vicinity, so it has been grazed lightly if at all by domestic stock. Its remoteness and lack of roads have kept out all but a few visitors, and until very recently there was no adequate program for the control of natural fires. Malay Gap lies at an elevation of about 7,200 ft, and represents a somewhat less productive site for the growth of pine timber than the other two locations.

The controlled burning program on the Fort Apache Reservation gave an opportunity for several special studies. Since 1950, more than 150,000 A of pine forest have been treated with controlled fire, primarily to reduce fire hazard. Secondary objectives are partial thinning and pruning of sapling stands, and improvement of forage growth.

These have been extensive, large-scale burns. Firing is done in late fall, after the first of the fall rains but before the surface litter is too wet to burn. Buttes and ridges are ignited at the top to permit the fire to burn slowly and evenly downhill. Roads, rivers, and openings are used as backstops to restrict the area of the burn, but no effort is made to limit the fire to small blocks of a few acres.

While the Indian Service foresters feel that in general these controlled burns have achieved their objectives, strong dissenting opinions have been voiced by others who have viewed the results. The objective of this paper is not to evaluate the manage-

ment accomplishments or the effectiveness of the present controlled burning program. It was possible, though, to take advantage of some of the treated areas to study the effects of fire on vegetation and soils. Although the planned fires burn later in the year than the majority of natural fires, the results of the controlled burns can aid in the interpretation of the role of natural fires in the forest.

AGE AND SIZE CLASS DISTRIBUTIONS IN OLD-GROWTH STANDS

DIAMETER CLASS DISTRIBUTIONS

In an uneven-aged forest with a balanced distribution of diameter classes, the proportion of trees in each class remains relatively constant with time. The diameter distribution usually takes the form of a falling exponential curve when number of trees in each class is plotted against d.b.h. On semi-logarithmic paper this relationship is a straight line.

The relationship between diameter classes may be visualized by dividing the number of trees in any one diameter class by the number in the next larger size class. In a stable, balanced forest, the resulting quotient is a constant. This constant may vary widely from stand to stand, depending upon species and environmental conditions. This definition of a balanced forest is called de Liocourt's Law, from the French forester who first formulated it (Meyer & Stevenson 1943).

The structure of the Southwestern ponderosa pine forest is actually that of an all-aged forest composed of even-aged groups, but in blocks of several thousand acres it can be regarded as an uneven-aged forest. Tree diameters derived, for instance, from a large scale timber inventory should be distributed according to de Liocourt's Law if the forest as a whole is properly balanced.

A detailed timber inventory of the Maverick Working Circle, Fort Apache Indian Reservation, was made available by Southwest Lumber Mills, Inc. This report included stand tables giving the average number of trees per acre by 2-inch diameter class for all stands distinctive in character or geographical location and of significant extent. These tables were based on data secured in 1951 and 1952 by Hammon, Jensen & Wallen Mapping and Forestry Services of Oakland, California. Modern photogrammetric techniques were combined with field data from random $\frac{1}{8}$ A sample plots to prepare this inventory. A similar timber inventory, made for the San Carlos Apache Tribe by K. B. Woods, Inc., of Portland, Oregon, was available for the Malay Gap area.

Stand tables computed from 165 survey plots in the Maverick area and 90 at Malay Gap show that these old-growth forests do not have the diameter structure expected in a balanced forest. On the best sites in the Maverick Unit, numbers of trees per acre in the diameter classes above 20 in. follow the expected linear relationship when plotted on semi-log paper (Fig. 3). The number of trees in the 4-in. class, the smallest recognized in the timber inventory, falls on the projected line of the larger trees.

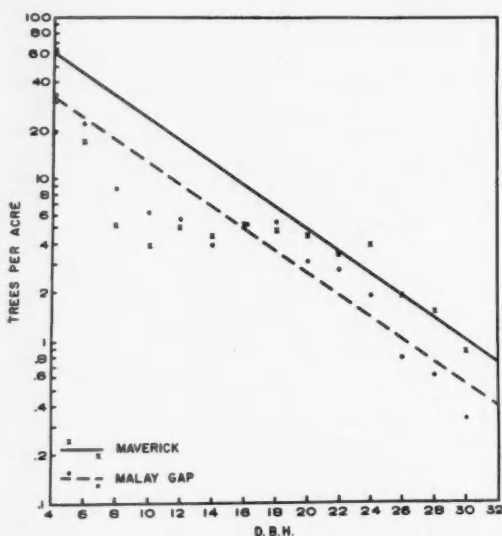


FIG. 3. Trees per acre as a function of diameter class at Maverick and at Malay Gap. Plotted points are the estimated number of trees in each diameter class as reported by timber inventory. Theoretical distributions are plotted from the larger size classes, according to de Liocourt's Law.

In all size classes between 4 and 20 in. d.b.h., there are fewer trees than are expected on the basis of the theoretical de Liocourt ratio. The same is true at Malay Gap. Numbers of trees in the size classes above 20 in., and in the 4- and 6-in. classes, plot on a straight line. Intermediate classes are somewhat deficient, although less so than in the Maverick Unit. The two lines plotted in Figure 3 are parallel, indicating that the same proportionate relationship between diameter classes is common to both areas. The difference in the position of the lines reflects the lower stand density at Malay Gap.

AGE CLASS DISTRIBUTIONS

Age data were obtained primarily from increment cores taken from most of the trees on a square plot of 10.24 A at Maverick, and on one of 5.12 A at Malay Gap. Mature trees were also sampled on a number of random plots established for other purposes. The sample trees were bored to the pith about 1 ft above the ground, and the cores were aged according to the methods developed by Dr. A. E. Douglass and his associates at the University of Arizona Laboratory of Tree Ring Research. The dating procedure is based on visual comparison of wide and narrow rings. Ring sequences tend to occur in a regular pattern, which can be used to locate certain key dates. This system has marked advantages over direct counting of rings. Both missing rings and double rings are common in ponderosa pine, and are apt to confuse the results of a direct ring count. Errors are inevitable even with a cross-dating technique, but the ages reported here are probably correct to within five years. To the age as determined from the core

must be added the length of time required for a seedling to grow to a height of 1 ft.

Ages are much more difficult to determine in a forest stand than are diameters. The sheer volume of work involved in boring trees and analyzing cores makes an extensive age sampling survey impractical. Ring counts on stumps, although often reported, are likewise unsatisfactory. Stump counts are ordinarily possible only on selective logging operations, where just the largest and least vigorous trees are cut. Even if all the trees are cut and their rings exposed, field counting of ponderosa pine rings is highly unreliable. Ages are best determined by use of accepted cross-dating techniques on properly surfaced cores.

An age class distribution could have been derived by calculating a regression equation relating the ages of bored trees to their diameters, and then applying the resulting regression coefficient to the stand table data from the timber inventory. There is so much variation in diameter within a single age class, however, that such an analysis would be almost meaningless. Pearson (1950:39) reported that trees in the 130-yr age class near Flagstaff ranged in diameter from 9.7 in. to 40.5 in., while those in the 246-yr class varied from 14.8 to 46.8 in. d.b.h.

Partial stratification can reduce the variability of age data. The Maverick timber inventory divided the trees in each diameter class into a number of subdivisions according to Keen tree class, a classification based on age and vigor of the individual tree. Four age classes are recognized, from immature trees to overmature veterans. Within each age class, four vigor classes are identified, depending upon size and thriftiness of the crowns. Thus there are a total of 16 possible classes. Trees of the same d.b.h. in a single Keen class are apt to be more similar in age than are those in an unstratified sample of the same size. Therefore, each sample tree bored for total age was classified according to the Keen system. For each of the 16 classes, diameter was plotted over age and a free-hand curve fitted to the points. The data were too few and too scattered to permit a satisfactory least-squares equation to be developed, particularly as the relationships were distinctly curvilinear. On the basis of the similarity of plotted points, the separate curves for some of the Keen tree classes were combined.

The final age-diameter curves were based on 107 trees from the Maverick area. From these curves and from the inventory stand tables, new stand tables were constructed for four of the distinct forest types distinguished by the timber inventory. These tables show the estimated number of trees and the basal area per acre contributed by each 20-yr age class (Fig. 4). Since the timber inventory included no trees less than 4 in. d.b.h., and since it takes at least 20 yrs for the average tree to reach 4 in., the 21- to 40-yr age class is the youngest included in the computations.

In each of the four age distributions shown in Figure 4, there is a relative lack of trees in the 100- to 120-yr age class, and an apparent overabundance

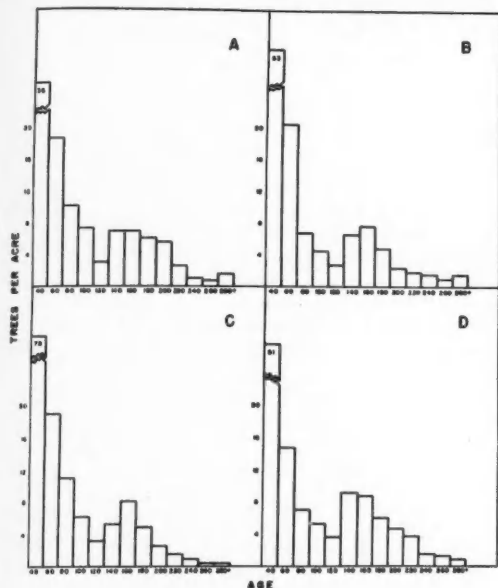


FIG. 4. Calculated number of trees per acre in each 20-yr age class in four selected stands at Maverick. Number beneath each bar is last year in age class.

in some of the older groups. An unbalanced age distribution is likewise evident on a single 10.24 A plot at Maverick (Fig. 5). This single plot was judged to be representative of the area as a whole, but it is by no means a random sample.

Just as important as the numerical distribution by age class is the proportion of the total ground space occupied by trees of each age class. At each of a series of random points at Malay Gap, the nearest tree in the dominant stand was bared for total age. The percentage of the total area dominated by trees of each age class was calculated from 42 sample points (Fig. 6). Sapling stands 21 to 40 yrs of age, and stands aged 100 to 180 yrs control most of the ground at Malay Gap.

It is the older trees which contribute the greatest basal area per acre at Maverick (Table 1). Basal area distribution by age class was calculated for four selected timber types of several thousand acres each. Trees aged from 140 to 200 yrs account for a high proportion of the total basal area in each, while the contribution of the intermediate age classes is low. The basal area of the youngest age classes is actually somewhat higher than that shown in Table 1, since the calculations on which the table is based included no trees less than 4 in. d.b.h.

In a balanced forest, the numbers of trees per acre in each age class should presumably follow somewhat the same exponential relationship as that postulated by de Liocourt's Law for diameter classes. Stand tables show a deficiency in number of trees in the intermediate age classes. The number of trees per acre in the youngest and in the older age classes are

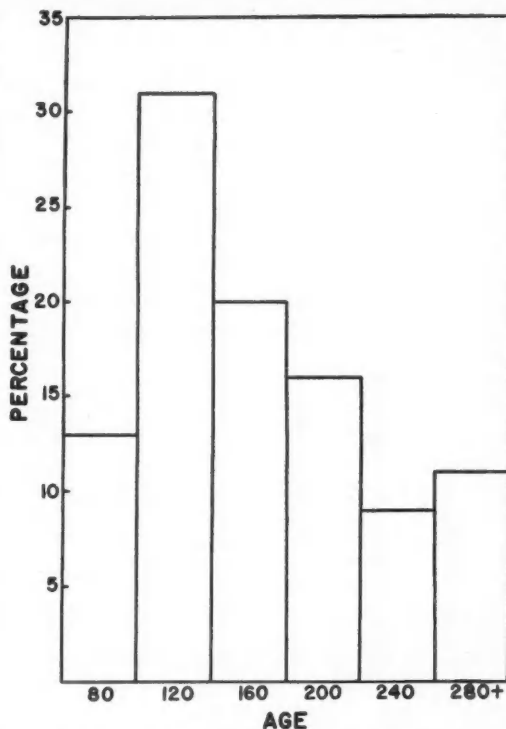


FIG. 5. Age distribution, by 40-yr age classes, of trees on intensively sampled 10-A plot at Maverick.

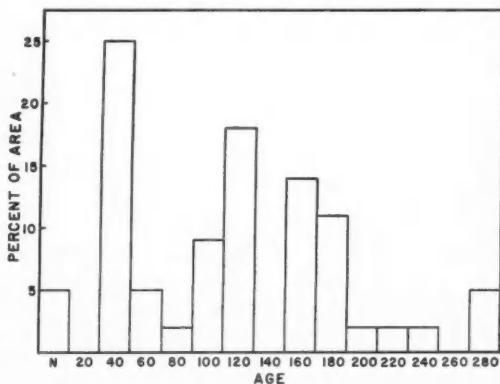


FIG. 6. Percentage of total ground area occupied by trees in each 20-yr age class at Malay Gap. N means non-stocked.

approximately those predicted by de Liocourt's Law, but the intervening classes fall far short.

If a forest is to maintain a stable age distribution over a long period, each of the important age classes must occupy approximately equal proportions of the available ground space. As a group of 120-yr-old trees grows into the 140-yr class, an equivalent area of 100-yr-old trees might be expected to grow into

TABLE 1. Basal area per acre by age class in selected stands, Maverick Unit.

Age Class (years)	BASAL AREA PER ACRE			
	Stand 1	Stand 2	Stand 3	Stand 4
	(sq. ft.)	(sq. ft.)	(sq. ft.)	(sq. ft.)
21-40.....	5.46	3.15	4.48	6.83
41-60.....	3.59	3.18	2.51	3.42
61-80.....	3.41	4.81	3.63	7.38
81-100.....	3.24	5.08	3.20	4.36
101-120.....	2.60	3.20	3.40	3.04
121-140.....	9.86	9.64	13.02	7.87
141-160.....	16.82	12.85	17.33	17.00
161-180.....	13.38	10.95	15.92	13.65
181-200.....	7.53	12.70	11.06	7.62
201-220.....	6.43	8.91	9.99	5.15
221-240.....	5.84	3.79	5.47	3.48
241-260.....	4.14	2.19	4.66	1.10
261+.....	8.45	9.34	5.50	1.91

the 120 yr class. The lack of area balance is evident in the stands sampled at Malay Gap.

Somewhat similar considerations apply to basal area of trees per acre. Lexen (Pearson 1950:28) derived the theoretical stocking density and space requirement for well-stocked stands of ponderosa pine. His table shows that fully stocked stands, regardless of the diameter of trees comprising them, have an average basal area of about 100 sq ft per A. Basal area in fully stocked stands remains relatively constant as the trees grow older, with mortality compensating for growth. It is therefore logical to assume that in a balanced forest, each age class will account for an equal percentage of the total basal area. It is evident from Table 1 that this is not the case at Maverick.

STRUCTURE AND GROWTH OF SAPLING STANDS

Young ponderosa pine stands of several ages were sampled at Maverick, at Bog Creek, and at Malay Gap. Circular plots were measured in fully developed, more or less uniform patches of reproduction, with the plot centers so placed that the entire plot fell within a sapling stand, of about the same density throughout. In no sense was this sampling technique designed to estimate the average number of trees per acre on the area as a whole. Rather, it was aimed at gathering information about the structure and composition of the reproduction clumps themselves. The samples are believed to be representative of a majority of the pine thickets in the study area.

Plot size, either $\frac{1}{40}$, $\frac{1}{400}$, or $\frac{1}{4000}$ A, was selected so that there were about 30 to 50 trees on each. Diameter at breast height of each tree was measured to the nearest $\frac{1}{40}$ in. On most of the plots, all trees under about 5 in. d.b.h. and many larger trees were felled, and a circular cross-section cut as near to the ground as possible. Increment borings, at about 9 in. above the ground, were taken from those trees that remained uncut. On a few plots, only a random sample of about one-fourth of all the trees was cut or bored. Only d.b.h. measurements and one or two

age borings were made on many of the Malay Gap plots. Heights of cut trees were measured directly, and standing trees were measured with an Abney level.

Growth data and past tree diameters were obtained from the increment cores and stump sections collected on the sample plots. The circular cross-sections were sanded to a high polish for ring analysis, while the increment cores were glued to grooved blocks for permanence and ease of handling. Diameters inside bark near ground level were measured on all sample trees as they were at the end of the 1957 growing season, and as they had been in 1947, 1937, 1927, and earlier decades. Details of the measurement procedure have been reported elsewhere (Cooper, in press).

The diameter measurements were used to compute the stem area of each stand at the time of sampling and at several earlier decades. It should be noted that this stem area was calculated from measurements of diameter inside bark near ground level, and it will be this that is meant whenever the words "stem area" are used in this paper. Where basal area is referred to, it will mean basal area calculated in the conventional manner from measurements of d.b.h. outside bark. A regression equation calculated from those stands for which complete data were available indicates that

$$B.A. = 1.20 S.A. - 19.9 \quad (1)$$

where B.A. is basal area in square feet per acre and S.A. is stem area measured in the same units. The standard deviation of the regression coefficient is 0.03. This equation is applicable to a range of basal area from about 100 to 300 sq ft per A. A less precise but more easily interpreted relationship states that basal area in these stands is 1.09 times stem area.

Obviously, stand data for previous years include only those trees present in the stand at time of final sampling, and conclusions about growth or stand structure specifically exclude any trees that died in the years between stand initiation and 1957. Total stand growth per acre in ten years is, of course, the difference between stem area at any two successive decades, while mean growth per tree is determined by dividing total periodic stand growth by the number of trees contributing to that growth.

DIAMETER CLASS DISTRIBUTIONS IN EVEN-AGED REPRODUCTION STANDS

Discrete even-aged groups, seldom more than one-half acre in size, are characteristic of the southwestern pine forest. In the dry climate of the Southwest, it is only in occasional years that seedlings can become established, so that virtually every tree in a single clump of sapling or pole size will have germinated in the same year. Once such an even-aged group develops, it is rarely possible for seedlings of succeeding year classes to become established within it. Diameter distributions in these even-aged pole stands may indicate some of the conditions under which the stands have developed.

Diameter distributions in even-aged forests have been studied by Meyer (1930), who fitted several mathematical series to diameter data. Jones (1945) suggested that the frequency distribution curve of diameter classes is of the binomial type, usually skew. More recently, Prodan (1953) has used the Charlier A-Function to describe diameter distributions. He constructed percentage frequency distributions of tree diameter, based on 2-cm diameter classes. The maximum percentage frequency, termed h_{max} , is used to characterize the resulting frequency curve. An h_{max} of 14 means that 14% of all the trees in the stand are included in the 2-cm class containing the most trees. Prodan presented a series of tables giving the expected diameter distribution for each integral value of h_{max} .

Diameter distributions of several ponderosa pine stands have been fitted to Prodan's theoretical values. Data from 197 trees in an 80-yr-old stand at Cooley Mountain fit the expected distribution quite closely (Fig. 7). The diameters of a group of 39-yr-old trees at Malay Gap likewise correspond closely to those predicted by Prodan's tables. The Cooley Mountain stand became established and made most of its early growth before white men came to the Southwest; the Malay Gap stands are in an area still little influenced by man.

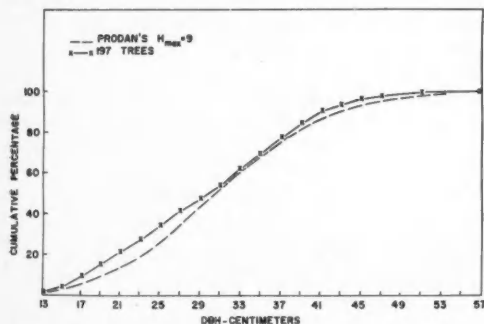


Fig. 7. Observed cumulative frequency distribution of diameters of 197 trees at Cooley Mountain, compared with distribution predicted from Prodan's theoretical relationship.

Diameter distributions of 33 stands sampled at Maverick and at Bog Creek deviate markedly from those predicted by Prodan's tables. In every case there are more small trees and fewer large ones than expected. The deviation is least in the 15 stands dating from the years 1903 to 1914, all of which were exposed to at least one and perhaps two fires at a very early age. The 18 younger stands, never touched by fire, show a greater preponderance of small trees.

A different approach has been used by Koyama & Kira (1956) in the study of the frequency distribution of individual plant weights. They concluded from experimental evidence that weights of seeds and very young seedlings usually follow a normal distribution.

They showed by a mathematical model that the exponential nature of growth processes can result in a log-normal distribution of plant weights. A test of this log-normal hypothesis shows that frequency distributions of basal area in several ponderosa pine stands rather closely approach a log-normal form.

Six classes were used for each stand. Class interval was determined by dividing the difference between the logarithm of basal area of the largest tree on the plot and that of the smallest by 6. A histogram was constructed, showing the proportion of the number of stems that fell in each of the six log-basal area classes.

A logarithmic frequency distribution was calculated for 197 80-yr-old trees at Cooley Mountain (Fig. 8). The logarithmic transformation means that the basal area limits of each class are 1.59 times those of the next smaller class (Table 2). The log-basal area distribution of the Cooley Mountain stands approaches the log-normal form, but is skewed toward the larger size classes. The histogram of the Malay Gap stands is similar in shape (Fig. 8). By contrast, the log-basal area histogram of the 1903-1914 Maverick and Bog Creek stands is somewhat skewed toward the smaller size classes. The younger stands from the same area show an even greater relative preponderance of trees in the smaller size classes (Fig. 9).

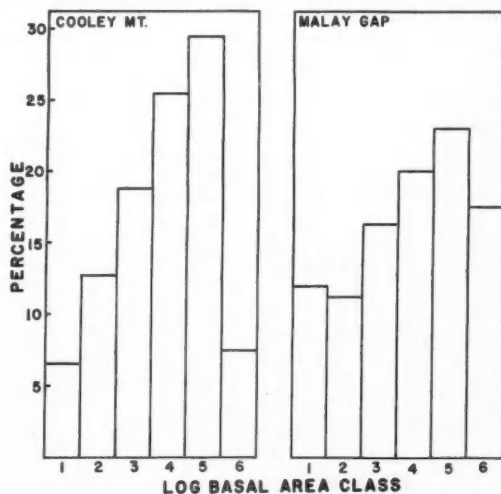


Fig. 8. Histogram of logarithm of basal area, Cooley Mountain and Malay Gap stands. Note that distribution is skewed toward the larger size classes.

AGE CLASSES OF REPRODUCTION STANDS

Only in occasional years of favorable weather can reproduction become established. The 1919 year class is conspicuous throughout Arizona, particularly around Flagstaff. It is present in the Bog Creek area, but is almost completely lacking further south at Maverick. Possible reasons for the lack of this important age class will be discussed later. Other

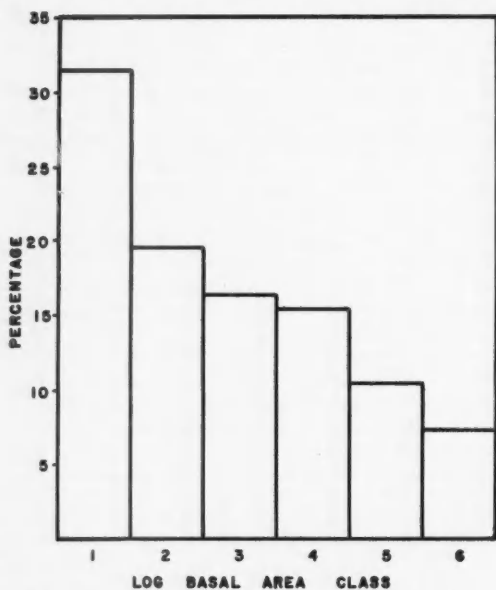


FIG. 9. Histogram of logarithm of basal area, Maverick stands never exposed to fire. Distribution is skewed toward smaller trees.

TABLE 2. Calculation of class interval for frequency distribution, Cooley Mountain.

	D.b.h.	Log basal area
Largest tree.....	21.4	0.39759
Smallest tree.....	5.3	9.18526 - 10
Difference.....		1.21233

Class interval = $1.21233 \div 6 = 0.20205$
 Antilog 0.20205 = 1.592 = class multiplier

classes recognizable in one or more of the areas studied are 1903, 1909, 1923, and 1928. A few small stands at Bog Creek originated in 1933. Trees of other ages are rare, and there are no extensive stands of saplings less than 25 yrs old. In part this is because there is little room in the densely stocked old-growth forest for young trees—the available space has been pre-empted by the heavy growth of earlier years. It is evident, though, that weather conditions in the White Mountains have not been suitable in recent years for the establishment of ponderosa pine reproduction.

RELATION OF MEAN GROWTH PER TREE TO STOCKING

At moderate stocking rates in young stands of ponderosa pine, mean growth per tree is evidently a function of available growing space and, perhaps, of the age of the stand. Age of stand, however, makes little difference in the amount of stem growth added at Maverick and Bog Creek. The stem area growth on each plot during the decade 1948-1957 was compared with the growth on the same plot in the pre-

vious ten-year period. A t-test applied to these paired comparisons showed no statistically significant difference in growth in the two periods; the computed value of *t* was less than one. At least in the age range from about 20 yrs to 55 yrs, the amount of stem area growth added by any one stand remains relatively constant from one decade to the next.

A linear regression equation can be closely fitted to the mean growth per tree of the Maverick-Bog Creek stands, if stands of extremely high and low density are omitted from the calculation. Based upon 25 stands supporting from 480 to 7700 stems per A,

$$g = 0.00309 + 52.6 \frac{1}{n} \quad (2)$$

where *g* is mean stem area growth per tree in 10 yrs, expressed in square feet, and *n* is number of trees per acre. Each individual observation used in the calculation of this regression was weighted by the reciprocal of stand density. This reciprocal is of course the same as available space per tree. The resulting equation accounts for about 92% of the observed variance in mean growth.

Stands with more than 7700 stems per A were omitted from this calculation because it was evident from the graph of the data that average growth of very dense stands deviated from a straight line. To demonstrate this fact, deviations from regression were computed for each of the 25 stands used in the original calculation, and also for the 6 overstocked stands omitted from the regression (Fig. 10). It is clear that as stand density exceeded about 6000 stems per A, growth deviated more and more from the calculated straight line. This point marked the beginning of stagnation.

There is certainly a minimum stocking rate below which growth per tree no longer increases. When the available space per tree exceeds that which the average tree can properly exploit, a further increase

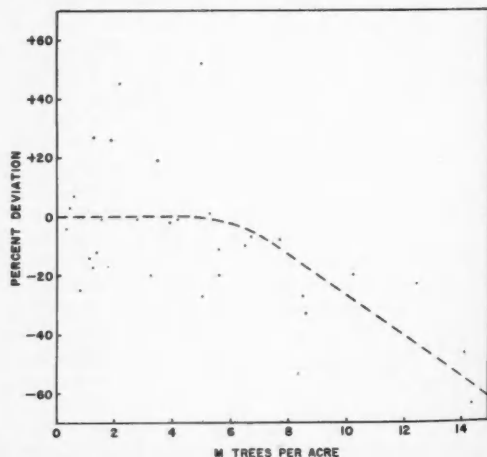


FIG. 10. Percentage deviations from regression equation relating mean growth per tree to stand density.

in spacing will yield no appreciable additional growth. Too few stands of very low density were included in this study to give much information on this point. It seems, though, that a decrease in stand density below about 450 stems per acre in 35-yr-old stands does not greatly stimulate growth.

Increment cores from several thrifty open-grown trees were used to estimate maximum growth rates in the absence of competition. Although mean growth per tree in moderately stocked stands remains relatively constant from one decade to the next, stem area growth of open-grown trees is directly proportional to age. Based on 39 observations,

$$g_0 = 0.0100 t \quad (3)$$

where g_0 is 10-yr growth in square feet and t is age at the midpoint of the growth period. It is apparent from plotting of the data that the range or spread of the observed growth values increases directly with age, so that the standard deviation of growth is directly proportional to age, and its variance to the square of age. It is therefore appropriate in the fitting of equation (3) to weight each observation by the square of age. The standard deviation of the resulting regression coefficient is 0.008.

A tentative idea of the maximum space that can be utilized by a single tree can be obtained by combining equations (2) and (3). The average age of the trees used in the calculation of (2) is 40 yrs, so that the age at midpoint of the 10-yr growth period is 35 yrs. It follows from the two equations that a spacing of about 150 trees per A in a 35-yr-old stand should yield the same growth per tree as that obtained from open-grown trees of the same age. Of course, trees in such an open stand would probably be of poor form and quality.

TOTAL STEM GROWTH PER ACRE

Total periodic growth per acre is closely related to stocking rate, but the form of the relationship is more complex than that of individual tree growth. Total stem area growth increases with stand density up to a point, and then decreases as number of trees per acre exceeds the optimum. A simple graph of stem area growth over stand density best demonstrates this relationship (Fig. 11). Growth increases rapidly with stand density up to about 4000 stems per acre, and then decreases slowly as stocking rate continues to increase. The curve is similar in shape to that shown by Gaines (1951) for longleaf pine. As in longleaf pine, growth of ponderosa pine stands is more closely related to number of trees per acre than to stand basal area.

The total basal area per acre is determined both by the number of trees per acre and by the age of the stand. Since basal area is a joint function of stand age and density, it is best visualized by plotting basal area over the product of number of trees per acre times age (nt). The resulting curve has its maximum at $nt = 160,000$ (Fig. 12). Substituting various values of t and solving gives an indication of the stand density that will produce the maximum

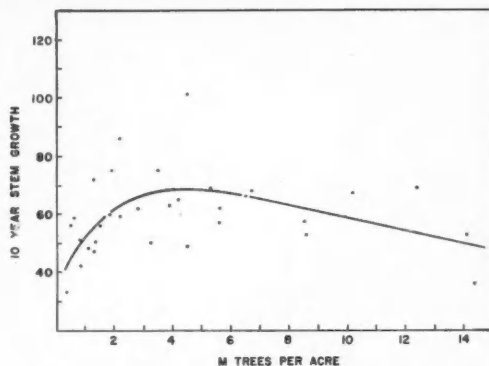


FIG. 11. Stem area growth in square feet per A in 10 yrs as a function of stand density.

basal area per acre at any given age (Fig. 13). According to this estimate, maximum basal area will be reached with about 6400 trees per A at 25 yrs, and with about 3200 at 50 yrs.

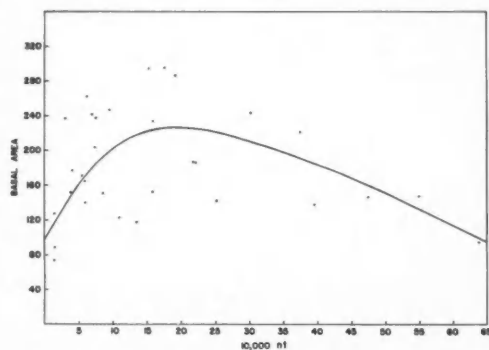


FIG. 12. Total basal area per acre as determined jointly by number of trees per acre (n) and by age of stand (t). Basal area is plotted over the product of trees per acre times age (nt).

The maximum basal area attained by these young stands is far in excess of the 100 sq ft per A that Pearson (1950) considered to represent full stocking. According to the Maverick timber inventory, average basal area on good sites is slightly more than 100 sq ft per A. This figure integrates mature groups, young thickets, and small openings. In small, uniform pole stands, basal area can easily reach more than twice Pearson's full stocking estimate.

DOMINANCE, SUPPRESSION, AND MORTALITY

The preceding growth studies have dealt with all trees in the stand, small as well as large. It is generally considered that the smaller trees in a stand, however, have little effect on the growth of the dominants. It has been almost universally accepted that as the dominant trees grow up and overtop the smaller, the losers in the competitive race are suppressed, retarded in their growth, and eventually

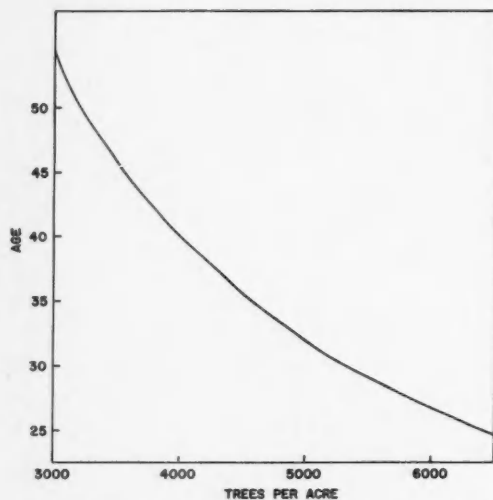


FIG. 13. Stand density at Maverick that is predicted to yield the maximum basal area at various ages.

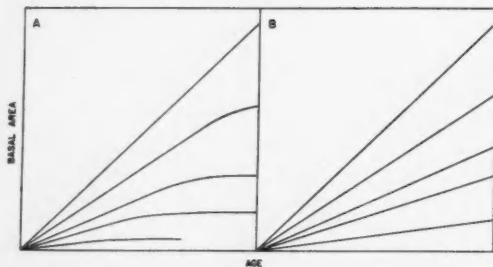


FIG. 14. The usual concept of suppression is shown diagrammatically on the left. The growth of the trees in a young stand of ponderosa pine is more adequately described by the fan-shaped pattern at the right.

eliminated from the stand. Therefore, the smaller trees are usually thought unimportant by comparison with the faster growing dominants and codominants.

This description of the suppression process is no doubt valid in those forests where the primary competition is for light. It does not, however, hold true in the ponderosa pine forests of the Southwest, where competition is mostly for water. As Pearson (1950) has pointed out, sunlight is much less likely to limit growth of ponderosa pine than is water supply. In the forests of the humid regions, once a tree is overtopped it becomes successively less able to secure the light energy needed for growth; hence it is suppressed and its growth nearly ceases. Where light is abundant and water is lacking, however, even small trees are usually able to secure their small but proportionate share of available soil moisture, so that the growth of small trees is not much retarded even by apparent suppression.

Small ponderosa pines grow slowly from a very early age, their growth increment remaining nearly

constant from one period to the next. Basal area of large trees likewise increases rather uniformly in successive periods. The growth of the trees comprising a stand of ponderosa pine more nearly resembles the fan-shaped pattern of Figure 14b than the more usual suppression pattern of Figure 14a.

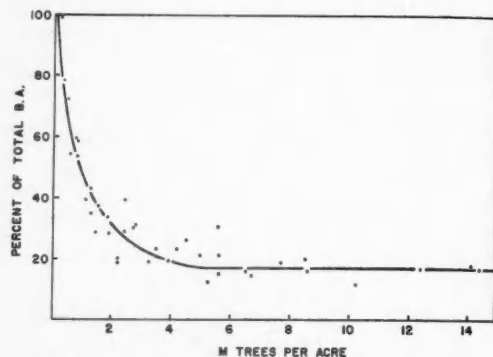


FIG. 15. Proportion of the total stand basal area contributed by the 400 largest trees per A in stands of varying density.

A statistical comparison of the growth of the smallest trees on a single plot with that of the largest trees on the same plot provides evidence of this growth pattern. Data for the 5 largest and the 5 smallest trees on a sample plot bearing 21 trees were used for this comparison. Stem areas in 1957, 1947, 1937, and 1927 were grouped for each set, and the resulting relationship tested for linearity of regression by a method suggested by Snedecor (1956:455). In neither the large trees nor the small ones was the departure from linearity greater than would be expected from chance variation alone (Table 3).

TABLE 3. Analysis of variance, linearity of growth of dominant and suppressed trees.

Source	5 LARGEST TREES		5 SMALLEST TREES	
	D.F.	Mean Square	D.F.	Mean Square
Linear regression . . .	1	9018.73	1	17.3556
Deviations from linearity	2	1.20	2	.0240
Error	16	289.20	16	.8809

Suppressed and intermediate trees evidently play a greater role in young ponderosa pine stands than is customarily attributed to small trees. The proportion of total stand basal area contributed by the smaller trees increases with stand density (Fig. 15). At low stocking rates, virtually all the basal area of a stand is contained in the 400 largest trees on each acre. The proportion of the total contributed by these larger trees declines as density increases, until with more than 5000 stems per A only about 17% of the basal area is due to the 400 largest trees. Approximately the same relationship applies to total

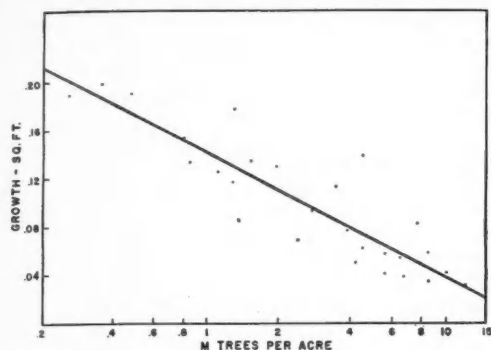


FIG. 16. Growth of the largest trees in each stand as a function of stocking.

periodic growth. The larger trees, which are often the only ones considered in growth analysis, add considerably less to total stand growth in young dense stands than do the great mass of small trees. The relative importance in stand growth and use of available water, nutrients, and light by any single tree in young ponderosa pine stands is roughly proportional to its size. This is unlike the situation in more humid forests where suppressed trees exert less influence on growth of dominant trees even than their dimensions would imply.

Concern has been expressed, by Weaver (1951a) and others, that the use of soil moisture by developing pine thickets may adversely affect the growth of the mature pine overstory. Several mature pines, more or less isolated within dense sapling stands, were examined at Bog Creek for evidence of this effect. Mature trees with poor crowns (e.g., Keen tree classes 3C, 3D, and 4C) could be expected to be most affected by competition from the sapling understorey. Increment borings from 6 such trees showed no unmistakable evidence of a change in growth pattern since origin of the sapling stands. Growth before and after that time was so slow as to be almost imperceptible. It may be, however, that the decline of these decadent trees was hastened by sapling competition.

In contrast to these results, Weaver (1959) has reported that on the Warm Springs Indian Reservation in Oregon, thrifty mature trees of Keen class 3B not subjected to understorey competition grew 23% faster than their counterparts within dense sapling thickets. Competition from the understorey affected immature pines of Keen class 2B even more strikingly.

Natural mortality in dense young ponderosa pine stands is surprisingly low, even among clearly suppressed trees. Examination of fire-killed trees of known age established that it is easily possible to identify every tree larger than 0.5 in. d.b.h. that has died within the past 6 yrs. On all the sample plots in reproduction stands, a tally of dead trees was kept (Table 4). Natural mortality of small suppressed trees less than one inch in diameter probably does not exceed 2% annually; in the larger size

classes it is much less. The uncertainty derives from the fact that there is no way of knowing how many years' accumulation of dead trees is included in the mortality tally. The figure of 6 yrs is no more than a guess. In this area of slow decay, identifiable dead trees may last even longer.

TABLE 4. Estimated natural mortality in last six years on sample plots.

	DIAMETER CLASS					
	Less than 1"	1.0-1.9"	2.0-2.9"	3.0-3.9"	4.0-5.9"	6.0-7.9"
Number of dead trees per acre...	470	184	31	16	8	2
Mortality as % of number in size class 6 years ago.	6.7%	4.0%	1.1%	0.8%	0.6%	0.7%

GROWTH OF POTENTIAL CROP TREES

The largest trees in the stand will comprise most of the dominant mature stand and will make up most of the eventual timber harvest in managed stands. It is of interest to consider the relationship of the growth of these dominants to stand density.

Growth of the largest trees in each stand is more closely related to the logarithm of stand density than to its reciprocal or to other measures used in the preceding analyses (Fig. 16). Measurements of trees on 27 sample plots show that for the 400 largest trees per A

$$g_L = 0.34 - 0.10 \log n \quad (4)$$

where g_L is mean stem growth per tree per decade in square feet, and n is number of stems per acre. The standard deviation of the regression coefficient is 0.033; the computed regression accounts for about 79% of the observed variance in mean growth of the largest trees.

GROWTH AND NEEDLE WEIGHT OF INDIVIDUAL TREES

Cable (1958) has shown that there is a logarithmic relationship between needle weight and diameter of individual mature ponderosa pine trees in central Arizona. The relationship of stem area growth to needle weight in young pine stands was investigated on two of the $\frac{1}{100}$ A sample plots at Maverick.

All trees were cut on these two plots, and the current year's crop of needles stripped from each tree. Sampling was done in early November after seasonal growth was completed. Needles were air-dried with the aid of a steam radiator, since no oven facilities were available. Stem area growth during the preceding ten-year period was determined from stump sections as before. The trees on one plot were about 49 yrs old; the other plot was aged 30 yrs. The 18 trees on the older plot ranged from 1.0 to 8.8 in. d.b.h.; the 24 on the younger plot were from 0.5 to 7.3 in. d.b.h.

Stem area growth on these two plots is directly proportional to needle weight, according to the equation

$$g = 0.00624 W \quad (5)$$

where g is 10-yr stem area growth of a tree in square feet and W is weight of the current year's needles in kilograms. There is no statistically significant difference in the regression equations applicable to the two stands despite their difference in age; hence the data from all 42 trees were pooled in the calculation of the final regression equation.

The direct relationship between needle weight and tree growth is to be expected, for needle weight is a measure of the quantity of photosynthetic tissue available for the elaboration of material to be stored as new wood. There is a definite difference in the weight of the current year's needles on the two plots: 1063 kg per A in the older stand, and 787 kg in the younger. An estimate based on only two trees suggests that about 40% of the green needles present in November, after needle fall is mostly completed, are of the current year's crop.

HEIGHT OF DOMINANTS AS A FUNCTION OF AGE AND STOCKING

Foresters have usually considered that height of the dominant trees of a given species varies much less with stand density than do tree diameters; hence height of dominants in relation to age is frequently used as a measure of site quality. Lynch (1958) has pointed out that in many instances height growth is very markedly affected by stand density. He concluded from a review of the literature that retardation of height growth by density of stocking is most apparent where root competition is most intense. Lynch went on to evaluate the effect of stocking rates on height of dominants in ponderosa pine stands in Washington and Idaho. He represented density of stocking as a proportion of the average density calculated from all his plot data. He found that tree heights are reduced as stocking percentage exceeds 100, and that the effect of stand density on height is much greater on poor sites than on good.

Lynch's method of relating height growth to stand density is not applicable to the present study, partly at least because the average stocking rate calculated from all the sample plots would still represent a generally overstocked condition. Instead, the mean height of the two tallest trees on each plot was considered as a function of stand age and stocking rate. For the 29 plots at Maverick and Bog Creek for which height measurements were available,

$$H = 100 - 18.8 \log n - 7.66 \frac{1}{t} \quad (6)$$

where H is height of dominants in feet, n is number of trees per acre, and t is age of stand in years. This equation accounts for 86% of the variance in height. If extrapolated far beyond the range of the

data from which it was derived, this equation indicates that the maximum attainable height of ponderosa pine trees at Maverick is 100 ft. Actually, fully mature dominants reach a height of about 110 ft.

PATTERN

A conspicuous feature of the ponderosa pine forest is the grouped arrangement of the trees. It is obvious that the forest is composed of distinct groups, each made up of several trees similar in size and apparent age (Fig. 17). This fact has long been recognized, but surprisingly little attention has been given to the structure of these groups or to their mode of origin.



FIG. 17. Typical stand of mature ponderosa pine, showing grouped distribution of trees.

An objective stand analysis technique is offered by the method of contiguous quadrats proposed by Grieg-Smith (1952). He suggested laying out a grid of 256 contiguous quadrats, and recording the number of plants falling in each. In analysis of the data, each pair of adjacent quadrats is combined, creating what amounts to a new grid of 128 blocks on the same area. The combining procedure is repeated several times to give the number of individuals per block when the blocks consist of 1, 2, 4, 8, 16, 32, 64, and 128 of the original small quadrat units. An analysis of variance is then carried out to determine the variance (mean square) attributable to each of these

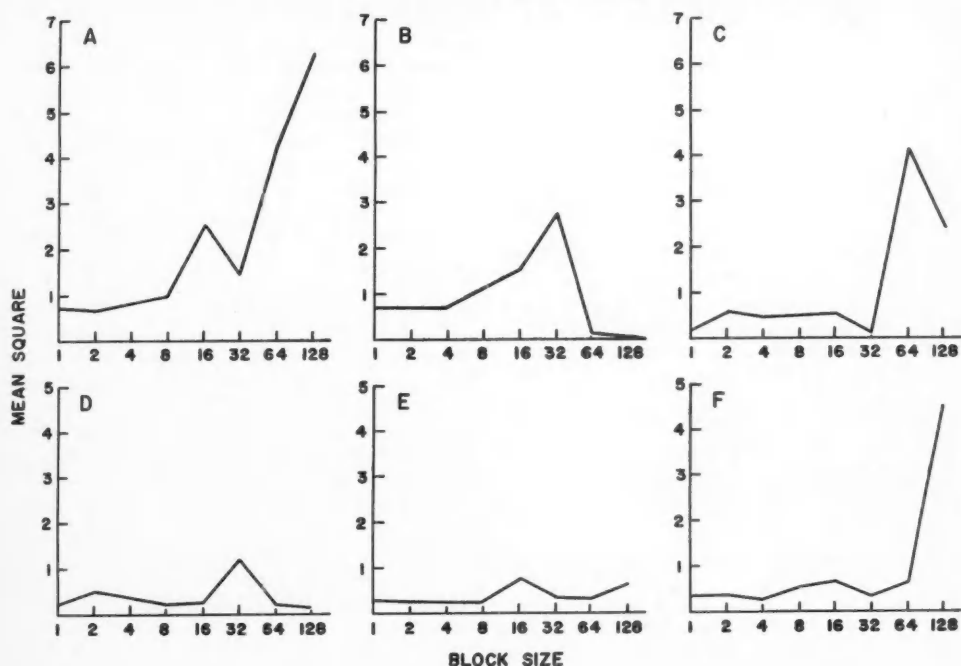


FIG. 18. Variance (mean square) attributable to blocks of different size, contiguous quadrat analysis of mature stand at Malay Gap (A, B) and at Maverick (C, D, E, F).

block sizes. If the vegetation forms a distinctly clumped pattern, the variance of the block size corresponding to the approximate mean area of the clump will be much higher than the variance due to other block sizes.

Testing of the significance of the variance for the various block sizes presents considerable difficulty. Grieg-Smith originally suggested using a variance ratio test to compare the mean square due to various block sizes with the mean square residual for single quadrats. Once the fact of non-randomness of vegetation is established, however, a variance ratio test is no longer appropriate. At the present stage of development of contiguous quadrat analysis, conclusions are best based on a subjective interpretation of peaks in variance. The consistent recurrence of a peak at about the same block size in a series of analyses gives a strong indication of its validity (Thompson 1958).

The theory underlying contiguous quadrat analysis assumes that the area of the plant is negligible in relation to the size of the quadrat. This is clearly not true in ponderosa pine. The use of $\frac{1}{100}$ A quadrats, however, makes plot size rather large in relation to all but the largest trees.

Four grids of 256 contiguous $\frac{1}{100}$ A quadrats were set up at Maverick, and two at Malay Gap. The largest block size was thus 2.56 A. In analyzing the pattern of the mature stand, only trees evidently older than 50 yrs were considered. Most of the six

grids show a pronounced peak in variance at block sizes of 16 or 32 quadrats (Fig. 18). Several of the grids also show a high variance at the largest block size. Little significance can be attached to the latter peaks because of the small number of degrees of freedom upon which they are based. There is only one degree of freedom associated with a block size of 128 quadrats, and two with the next smaller block size. The large variances at the bigger block sizes may be due to chance alone, or they may be associated with a larger scale pattern of vegetation.

Contiguous quadrat analysis indicates that the trees comprising the mature stand at both Maverick and Malay Gap are aggregated into groups with an area of .16 to .32 A. This is consistent with what has already been observed about the clumped distribution of ponderosa pine.

A similar analysis was made of the reproduction stand on the same six 2.56 A plots. It seemed inadvisable, because of the great difference in size of individuals, to combine both the mature stand and young trees in a single computation. All trees over 2 in. d.b.h. were included in the reproduction tally (Fig. 19). As in the mature stand, the Malay Gap grids show a pronounced peak at a block size of 16 to 32 quadrat units. The average clump size of young trees at Malay Gap is about .16 to .32 A.

The Maverick grids show an evident peak at about the same block size as at Malay Gap. The main peak, however, is at 64 quadrat units, reflecting the

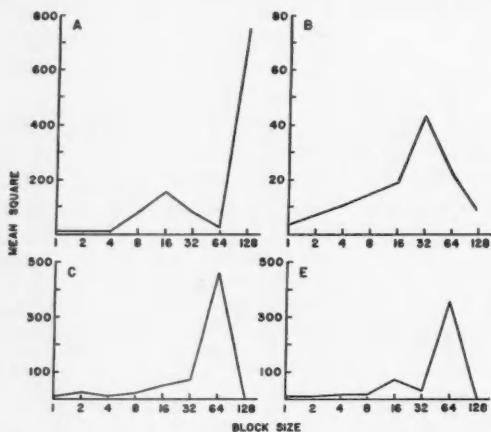


FIG. 19. Variance (mean square) attributable to blocks of different size, contiguous quadrat analysis of reproduction stand at Malay Gap (A, B) and at Maverick (C, E).

large patches of reproduction that are clearly evident at Maverick. Within these large patches are smaller clumps of thriftier and more vigorous trees. The smaller sub-groups are indicated by the peaks at 16 and 32 units.

FOREST CONDITIONS AT MAVERICK AND AT MALAY GAP

Although similar in basic composition and structure, the forests at Maverick and at Malay Gap are quite different in appearance. A visitor to Malay Gap, conditioned by acquaintance with the over-dense thickets characteristic of most of the Southwestern pine region, is immediately struck by the open nature of the forest (Fig. 20). The forest floor is carpeted with a deep layer of grass, and small discrete patches of young trees are dispersed among groups of stately pines. The pure beauty of the Malay Gap region more than compensates for its difficulty of access.



FIG. 20. Typical view of the ponderosa pine forest in the primitive area at Malay Gap.

The site at Malay Gap is clearly not as good as that at Maverick. The average height of mature dominants at Malay Gap is about 95 ft, while those at

Maverick average about 110 ft. The height of dominants in sapling stands averages 10 to 12 ft less than in stands of comparable age and stocking density at Maverick. According to the Malay Gap timber inventory, the average basal area of the mature stand is about 70 sq ft per A on the most densely stocked 8200 A. By contrast, the mean basal area of the 13,000 A timber type including all the Maverick study plots is about 102 square feet per acre. The difference reflects inherent differences in site productivity.

Until recently, lack of adequate transportation has prevented an effective fire control program at Malay Gap. Weaver (1951a) found from analysis of fire scars that fires had swept across Malay Gap in 1943, 1935, 1919, 1910, and about every 7 yrs before that time. Fire scars on living trees indicate that at least the last two fires were very extensive and covered most of the area. By contrast, the areas studied at Maverick and Bog Creek have either been free of fire since stand origin, or have been protected since a fire in 1924. Differences in site quality and in fire history are the primary differences between Maverick and Malay Gap. To determine how each of these factors has affected stand structure, it is necessary to examine some of the ecological effects of fire in ponderosa pine.

FIRE IN THE ECOLOGY OF PONDEROSA PINE

A number of recent studies on the relation of fire to ponderosa pine have been reported by Harold Weaver. On the Colville Indian Reservation in eastern Washington, he examined a group of 40-yr-old pine stands. One portion of the study area was burned by a wildfire in September, 1914, when the young pines were about 11 yrs old; the other portion had been protected from fire throughout its life. Thirty years later, the unburned area was covered by a stagnated stand of saplings so thick in places as to be almost impenetrable. There was an average of 14,800 stems per A on plots in the unburned area, with a mean d.b.h. of 1.7 inches and a height of 12.3 ft. Stand density in the stocked portion of the fire-thinned area was 1100 stems per A, the trees averaging 7.4 in. in diameter and 32.2 ft in height. Only about 9% of the burned area was stocked, the result of a hot fire burning out of control (Weaver 1947). In the Southwest, exclusion of fire has likewise induced the formation of dense thickets which give every impression of near stagnation (Weaver 1951a).

As a consequence of long continued fire exclusion, fire hazard has built up until the stage is set for a devastating conflagration (Weaver 1951a, 1955). The dense reproduction stands are themselves highly inflammable. A heavy needle mat has accumulated, and snags and dead wood have added fuel. Without periodic fires to remove this debris a little at a time, it has built up to a point where any fire is liable to race uncontrolled through the treetops. Weaver believes this increase in fire hazard to be the most potentially dangerous change that has occurred since early days.

In June, 1956, a spark from a logging operation

set off a fire that ran out of control through 21,000 A of ponderosa pine forest north of the Mogollon Rim. The behavior of the fire and the meteorological conditions accompanying it were analyzed by Schaefer (1957). He described the Dudley Lake fire as a classic example of a fire accelerated by local air subsidence and a low-level jet current. The hot, dry winds resulting from these unusual conditions lead to an explosive situation in which even the most modern fire fighting equipment is ineffectual once a conflagration gets under way. Yet it is possible to argue that the Dudley Lake fire would not have killed virtually every tree that it touched had not the forest fuel been allowed to accumulate for 40 yrs and more. Surely local air subsidence and jet streams have recurred throughout history, but there is no clear evidence of past holocausts of the magnitude of Dudley Lake in the ponderosa pine forest. The Dudley Lake fire was touched off by logging and not by lightning; but there is no reason to doubt that Indians built campfires in the woods even in the hot, dry days of June.

Preliminary test of prescribed burning in Arizona (Weaver 1952) showed that lighter fuels such as fallen needles, branches, and cones were reduced approximately 55% by weight, while the cubic foot volume of logs and stumps declined 64% to 80%. Four years later, though, the quantity of fuel on the ground equalled that before burning (unpublished data on file at Fort Apache Agency, Whiteriver, Arizona). Part of this increase is attributable to the fact that 30 yrs of fire exclusion prior to the experimental burns had allowed an abnormal number of live needles to remain on the lower portions of the tree crowns. Light fires which do not ignite the crown generally singe the lower needles, which then fall from the tree. The height of the needle scorch resulting from a low intensity fire is a function of the initial vegetation temperature and of the height of the flames above the ground (Byram 1958). Live needles extended to within a few feet of the ground on the Fort Apache experimental burning plots; these needles were singed by the fire, fell to the ground, and added their bulk to the quantity of fuel on the forest floor after the prescribed burn. A second fire might produce a more long-lasting fuel reduction.

This burning experiment evaluated only the effects of fire on dry fuel lying on the ground. Of equal importance is the effect of repeated fires on the hazards represented by sapling stands, which are highly subject to destruction by crown fires. Crown fires are of two types: dependent, which require heat from surface fuels to preheat and ignite the crown, and independent, in which the fire travels directly from crown to crown without aid from surface fuel combustion. Most crown fires observed in the Southwest on relatively level ground are dependent. The likelihood of crown ignition resulting from a surface fire is a function of the height of the base of the crown above the flames. If, for instance, there are no needles below the 12-ft level, the crowns of a sapling stand

are much less likely to be ignited by a surface fire than if the crown level is at a height of 6 ft. The quantitative effects on fire spread and severity of the raising of crown level are not known, but they are evidently considerable. It is well known that the intensity of radiated heat varies as the square of the distance from the source. In a surface fire in a sapling stand, though, this relation is greatly complicated by heat convection.

If a crown fire should start in a sapling stand, it is not apt to run as far or as fast if some of the fuel has been removed as in a solid stand of dense saplings. Experience on the Fort Apache Reservation has demonstrated that it is easier to fight a wild-fire in an area previously treated with controlled fire than in untreated areas. In summary, long continued fire exclusion has increased the danger of destructive wildfires in three ways: by permitting excessive buildup of dry fuel on the forest floor, by leaving the tree crown level near the ground where ignition of live needles is more likely, and by permitting the formation of dense uninterrupted sapling stands over wide areas.

STAND STRUCTURE AT MAVERICK AND AT MALAY GAP

The young trees at Malay Gap are arranged much more definitely in groups than at Maverick, and only rarely do they grow under or very close to the trees of the mature stand. On only 10 of 512 quadrats were young trees more than one inch in diameter found growing on the same $\frac{1}{100}$ A plot as a mature tree. By contrast, 84 out of 1024 similar quadrats at Maverick had reproduction and mature trees growing on the same plot. The association of mature trees with young trees was tested for both stands, using a chi-square test on a 2 by 2 contingency table. Chi-square values for both the Maverick and the Malay Gap tables were highly significant, indicating a strong tendency for reproduction and mature trees not to be associated on the same quadrat. Chi-square values were much larger, however, for the Malay Gap tables than for the Maverick data. Only trees larger than 1 in. d.b.h. were considered in this analysis. There are many stunted and suppressed trees 2 to 6 ft tall growing under the mature overstory at Maverick. Most of these trees are at least 20 yrs old, and some are more than 30. Trees of this type are almost totally lacking under the Malay Gap overstory.

The lack of trees under the mature stand is evidently the result both of competition and of the periodic fires that have swept the Malay Gap area. Even under the open canopy of a mature forest, seedlings grow poorly (Fig. 21). Though the trees remain alive, they are stunted and unhealthy. Root competition, rather than competition for light, is apparently the governing factor. Root grafts between adjacent trees of the mature stand may play a part, although there seem to have been no studies of this subject in ponderosa pine. Yli-Vakkuri (1954) found that in even-aged stands of Scotch pine in Finland, many middle-aged trees had root grafts with the root systems of neighboring trees. Sometimes a network of

10 or more trees is formed by grafting, and water and nutrients are transferred through grafts from one tree to another. It is possible that there is a similar interconnection of the root systems of a mature even-aged group of ponderosa pines. If so, the united root systems may ramify so completely through the soil that newly established trees are unable to compete effectively.



FIG. 21. Stunted trees, 18 yrs old, growing under a mature group of pines at Maverick. Tallest of these trees is less than 3 ft high.

When a light surface fire passes through the forest, the stunted trees growing beneath the pine overstory are too small and weak to withstand its effects. A fire intensity that would injure a thrifty sapling little if at all is often fatal to a suppressed tree of the same age. More important, though, is the effect of needle fall from the mature stand. A considerable volume of light fuel rapidly builds up beneath the mature stand. When ignited, this fuel generates enough heat to kill any young trees which may be growing in its midst. By contrast, the lesser fuel accumulation in openings makes a less intense fire which saplings are able to survive. Evidence for this differential removal of trees under the forest canopy is provided by many observations on the controlled burns on the Fort Apache Indian Reservation. Virtually every seedling and sapling beneath mature trees is killed by the controlled burns, while nearby reproduction stands remain almost intact.

The failure of reproduction to survive under the mature canopy in the presence of fire largely accounts for the difference in pattern of smaller trees between Maverick and Malay Gap. Contiguous quadrat analysis demonstrated the existence of definite reproduction groups, .16 to .32 A in size, at Malay Gap. At Maverick, on the other hand, stunted reproduction is widespread beneath the mature trees, becoming much more vigorous in the openings (Fig. 22). This accounts for the peaks at two block sizes in the mean square diagram of Figure 18.

It has been asserted that the small trees growing under the mature overstory represent valuable advance reproduction which will greatly speed up stand regeneration following timber harvest. Actually, it



FIG. 22. Typical stand at Maverick, protected from fire since 1924.

is doubtful if these stunted trees will respond to release at all. Establishment of seedlings some 6 or 8 yrs before cutting the mature trees, if possible, is almost certainly good forest practice, but the stunted little trees 20 and 30 yrs old that often grow in the shade of the mature stand are probably more of a hindrance than a help to future forest growth.

There are many more trees per acre, particularly in the smaller size classes, at Maverick than at Malay Gap. On the 2.56 A plots at Maverick, there are almost twice as many trees in each of the size classes from 1 to 8 in. d.b.h. as on comparable plots at Malay Gap (Table 5). The numbers of trees larger than 9 in. are much more nearly equal on the two sets of plots, the slightly larger number at Maverick closely reflecting better site quality.

TABLE 5. Number of trees per acre in diameter classes from 1 to 14 in. on sample plots at Maverick and Malay Gap.

d.b.h.	TREES PER ACRE	
	Maverick	Malay Gap
1.....	241	110
2.....	141	83
3.....	79	46
4.....	61	38
5.....	26	10
6.....	18	6.2
7.....	9.3	3.6
8.....	7.0	2.8
9.....	4.4	4.4
10.....	2.1	1.4
11.....	1.7	3.0
12.....	1.9	3.6
13.....	2.2	3.0
14.....	1.4	2.4

Although the small plots in reproduction stands were not intended as a quantitative estimate of stand density on the area as a whole, it is significant that the average number of trees per acre on the Maverick-Bog Creek plots is two to four times as great as on plots of comparable age at Malay Gap (Table 6). It has already been pointed out that the Maverick

TABLE 6. Summary of sample plots in reproduction stands

Location	Year of Origin	No. of Plots	STEMS PER ACRE BY DIAMETER CLASS							Total
			Less than 1"	1.0-1.9"	2.0-2.9"	3.0-3.9"	4.0-5.9"	6.0-7.9"	Over 8.0"	
Bog Creek.....	1919	8	4280	2257	1102	623	422	63		8748
Maverick.....	1928	9	1522	1353	604	471	369	47		4367
Malay Gap.....	1914-19	13	332	400	605	488	355	115	15	2311
Malay Gap.....	1928	8	435	400	415	335	265	60		1910

and Bog Creek plots have a much higher proportion of small trees than those from Malay Gap. The Malay Gap plots have the most trees in the largest size class, despite the definitely poorer site.

The densest stand sampled at Bog Creek had the equivalent of 14,400 stems per A in a 38-yr-old stand. The average density of seven 1919 stands at Bog Creek was almost 9000 stems per A. This figure is probably more or less representative of the mean density of pine thickets in the White Mountains. A series of twelve 2.5-A plots established in connection with the Fort Apache controlled burning program carried an average of 4855 trees less than 3.5 in. d.b.h. per A (unpublished data on file at Fort Apache Agency, Whiteriver, Arizona). These 12 plots were in a stand of ponderosa pine logged in 1924, and included the usual mixture of openings, reserved tree groups, and pine thickets common to cutover areas. It is likely that stand density on that part of these plots actually stocked with reproduction would approach the 9000 per A found on the Bog Creek plots.

Sapling stands of 1919 age support more trees per acre than do younger plots that would normally be expected to carry more trees (Table 6). Evidently conditions in later years did not permit as high a percentage of seedling survival as in 1919. At any rate, the average stand density on 9 sample plots in 1928 stands at Bog Creek is 4867 trees per A, about half that on the 1919 plots.

FIRE EFFECTS ON SAPLING STANDS

Much of the difference between the virgin area and the managed forest is due to the fires that have continued at Malay Gap. Natural surface fires have long been a part of the environment of the pine forest. What has been the role of these natural fires in the development of the forest? Equally important, what has been the effect on stand structure of forty years and more of fire exclusion?

A partial answer to these questions might be offered by an analysis of the results of the Fort Apache controlled burning program, but these burns have been carried out in stands that are no longer normal. Forty years of complete protection from fire have permitted the development of thickets with an abnormal number of trees per acre and an abnormal accumulation of fuel. A surface fire run through such a thicket is much different in its effects than if the stand has been burned at frequent intervals throughout its life.

Other prescribed burning experiments are slightly more informative. A 20-A tract of overstocked ponderosa pine thickets in north-central Washington was treated with controlled fire in 1942, and the results evaluated in 1950 (Morris & Mowat 1958). Future crop trees, those that are likely to constitute the mature stand of the future, were selected on the basis of size and vigor. The crop trees on the burned area grew 36% more in diameter and 7% more in height than those on the unburned plots, while the number of trees that offered significant competition to the selected trees was reduced from 2,410 to 895 per A. The authors concluded that prescribed fire, properly applied, can reduce competition among trees in dense ponderosa pine thickets and increase the growth of potential crop trees. The thinning was not uniform or selective, and occasionally destroyed all saplings in some poorly stocked portions of the stand.

The effects of natural fires on reproduction stands were studied at Malay Gap. Recorded fires have passed through that area at least 3 times in the lifetime of the present sapling stands: in 1919, in 1935, and in 1943. More recently, the B.S. Gap Fire of September, 1956, covered several hundred acres in the same area. This was a moderate surface fire apparently typical of those that have occurred many times in the past. The area burned faced to the north, on about a 15% slope. Weather records from Maverick Lookout, 8 mi northwest at about the same elevation, show that relative humidity was low and temperature high in the days preceding the fire. The fire danger rating, a numerical value that integrates fuel moisture, humidity, temperature, and wind, was almost as high in the three days preceding the fire as at the peak of the spring dry period. The B.S. Gap fire burned under severe, if not extreme, fire hazard conditions.

When the fire area was examined in September, 1957, the scorched needles, although brown and dry, still remained on the trees. It was thus possible to assess the amount of direct damage to tree crowns. Completely dead trees were also easy to detect. Lynch (1959) has reported on a study of mortality following fire in a 30- to 40-yr-old stand of ponderosa pine in eastern Washington. He found that mortality was correlated with degree of crown damage and with tree size. Most of the mortality occurred in the first year following fire, and most of the first-year mortality was caused by crown burning. There was sig-

nificant mortality the second year as well, mostly due to direct damage to the cambium.

The trees examined after the B.S. Gap fire had gone through only one growing season since the fire. Some additional mortality is to be expected, but the first-year effects will give a strong indication of the action of a natural fire on pine reproduction stands.

A large proportion of the trees less than one inch in diameter was killed by the fire. There were fewer of these small trees to begin with than on comparable plots in the unburned forest at Maverick and Bog Creek, and fewer still survived the 1956 fire. A progressively smaller proportion of trees was killed in each larger diameter class. Only 18% of the very small trees survived, whereas 84% of the stems in the 4- to 6-in. class remained and no trees over 8 in. d.b.h. died on any of the plots in the first year following the fire. No trees larger than 14 in. d.b.h. were observed to have been killed anywhere in the fire area. The first year effect of the B.S. Gap fire on the reproduction stand is expressed by the equation

$$P = 0.61 - 0.66 \log D \quad (7)$$

where P is the proportion of the total number of trees of a given size killed by the fire, and D is d.b.h. in inches. This equation is of course strictly applicable only to this one fire. While the absolute number of saplings killed may vary from fire to fire, somewhat the same proportionate relationship between size classes can be expected to be maintained.

The B.S. Gap fire removed about one-fourth of the basal area of reproduction stands. The relationship between basal area of 15 sampled stands before and after the fire is

$$B_t = 0.77 B_o \quad (8)$$

where B_t is stand basal area one year after the fire and B_o is basal area before the fire. The standard deviation of the regression coefficient is 0.065. The average basal area found from the 15 plots was 96 sq ft per A before the fire and 76 afterwards. Once again, these figures do not purport to represent the average basal area of the forest as a whole, but rather that of homogeneous clumps of reproduction.

The 1943 fire at Malay Gap reduced several representative sapling stands to a total basal area of 40 to 80 sq ft per A, as revealed by analysis of stump sections. Fourteen years later the basal area of each of these stands had approximately doubled.

MECHANISM OF THINNING BY FIRE

The differential killing of the smaller stems by fire constitutes a fairly effective thinning from below, which removes many of the small trees that lose out in the race for dominance. In the absence of fire, suppressed saplings tend to hang on and on, each taking at least a small portion of soil moisture at the expense of the dominants.

Natural fires thin sapling stands in three ways. Occasionally the surface fire becomes so hot at the base of a tree that the cambium is killed and the tree girdled. As far as could be told from a superficial

field examination, none of the trees on the B.S. Gap fire plots were killed in this way. A certain amount of mortality from this cause may be expected in the second year, however (Lynch 1959).

A second and much more common effect is the thinning of stands by the raising of their crown level. On most of the burned plots at Malay Gap there was a definite zone of scorched needles killed by the heat of the surface fire. Above the scorch line there was little if any needle damage. Obviously, if a suppressed sapling is 10 ft tall and a surface fire kills all needles below the 12-ft level, the small sapling's chances of survival are slim indeed. Most natural fires occur at a season when active growth is taking place, or at least when bud dormancy is not fully established. Under these conditions, heat generally kills buds as well as foliage.

On 10 of the 15 burned plots there was a noticeable raising of the crown level. In one stand with an average height of 27 ft, a crown level formerly at a height of 16 ft was raised to 24 ft. On the other plots, a smaller proportion of the live crown was scorched.

The periodic raising of the crown level and the killing of lower branches by fire aids in the natural pruning of ponderosa pine. This species prunes itself rather poorly, and lower branches tend to remain alive even in dense stands. Fire may be an important agent in the production of clean-boled trees, not so much by actual combustion of lower branches as by killing them so they fall naturally.

A third form of thinning is the killing of trees by the heat of a fiercely burning log or stump. The trees for several feet in every direction are frequently killed and small openings formed in this way. Such openings are seldom large enough to be detrimental to the growth of the stand. Roots of the surrounding trees quickly appropriate the vacant soil space and growth of the remaining trees may be stimulated.

Only rarely will local crowning of a general surface fire destroy a whole patch of young trees. On the B.S. Gap fire no stands were found that had been completely killed, although some were thinned too severely. There is evidence elsewhere at Malay Gap, however, of a number of apparently thrifty reproduction stands that have been totally wiped out, evidently by the fire of 1943.

It seems clear that a fire can and does pass through an established reproduction stand without destroying it. How, though, is it possible for a stand to become established in the face of repeated fires? Seedlings a foot or two high are extremely sensitive to fire, and even up to a height of six feet or more, it is doubtful if a young tree can withstand a surface fire of normal intensity.

Apparently they do not have to. In the normal forest there are many openings in which seedlings become established. There is little accumulation of pine needles or other dry material to carry a fire through these openings. The seedling stand itself does not produce enough dry material to carry a sur-

TABLE 7. Stems per 1/100 acre before and after controlled burning in young stand, Horse Mesa.

Plot No.	Age at Time of Fire	HEIGHT CLASS AT TIME OF FIRE																		Total	
		<1'		1-2'		2-3'		3-4'		4-5'		5-6'		6-7'		7-8'					
		Pre-Burn	Post-Burn	Pre-Burn	Post-Burn	Pre-Burn	Post-Burn	Pre-Burn	Post-Burn	Pre-Burn	Post-Burn	Pre-Burn	Post-Burn	Pre-Burn	Post-Burn	Pre-Burn	Post-Burn	Pre-Burn	Post-Burn		
1.....	11	18	9	40	11	51	24	22	11	4	4							135	59		
2.....	11	0	0	17	0	29	10	18	10	11	6	1	1	1	1			78	28		
3.....	11	16	4	1	1	2	1	6	5			2	2			1	1	28	14		
4.....	11	1	0	6	1	8	6	9	5	11	8	5	5	6	4			46	29		
5*.....	5			2		5		7		2		3		1				20			
6*.....	11	4		8		21												33			

* Not burned.

face fire until it is about 8 yrs old. Even then, there is usually only enough fuel to support a light and spotty fire.

Evidence for this hypothesis is hard to find because of the scarcity of very young pine stands. There are almost no extensive stands of waist-high trees suitable either for experimental burning or for observations of the results of past burns, except for a few small patches on Horse Mesa, east of White-river.

Horse Mesa was treated with controlled fire in the fall of 1954, 3 yrs before the examination. Six $\frac{1}{100}$ A plots were examined (Table 7). Trees on 5 plots were 11 yrs old at the time of the fire, and on one they were 5 yrs of age. The 5-yr-old stand and one of the 11-yr-old stands were not touched at all, even though the fire reached to within 50 to 100 ft in every direction. The obvious reason was lack of sufficient fuel. There was not much grass in the shade of the little trees, and they had dropped few dry needles. The slight fuel accumulation under the other 11-yr-old stands was sufficient to support only a relatively cool fire. This fire eliminated a greater proportion of the stems on the more densely stocked plots than on those that were more open, but the trees killed were mostly in the smaller size classes. The denser stands evidently produced a greater volume of needles which generated a locally hotter fire than that in the more open stands. The least dense of the 11-yr-old sample plots had so little fuel on the ground that fire did not spread to it at all. Any thinning would have left this plot seriously understocked.

Intensity of fire in very young stands seems to be sort of self-regulating feedback mechanism that provides the needed degree of thinning. Where there are many trees per acre, the volume of dry fuel builds up faster and to greater quantities than where trees are sparse. The greater fuel accumulation in turn supports a hotter fire that thins the stand in proportion to the fire's heat. As in older reproduction stands, it is chiefly the smaller trees that are removed by fire—almost no trees in the largest size classes were killed on the Horse Mesa plots.

EARLY GROWTH OF THE PRESENT MATURE STAND

One of the more significant problems to be considered in evaluating changes in forest conditions over the past century is the early growth of those trees that comprise the present mature stand. The growth pattern of these trees was presumably governed in their sapling stage by the same factors that control the growth of young stands today.

Growth of 104 trees more than 100 yrs old on the Maverick plots was analyzed from increment cores. From each core, 2 tree diameters were derived, one at about 25 yrs of age and the other just 20 yrs later. These diameters were used to compute the stem area growth during a 20-yr period in the early life of each tree. A 20-yr period was chosen to minimize the effects of brief chance variations in weather. It has already been demonstrated that in the age range from 20 to 55 yrs, stem area growth in a single tree remains relatively constant from one decade to the next. It is therefore legitimate to divide the calculated 20-yr growth by 2 to estimate the mean 10-yr growth during the early life of the present mature stand.

This estimated 10-yr early growth of the 104 mature trees was compared with the graph of growth of the largest trees in the present day sapling stands (Fig. 16). Two assumptions were involved here: that the trees now comprising the mature overstory were the largest, dominant trees in the stand when they were saplings; and that the same factors that now govern the growth of dominant trees in sapling stands were operative a century and more ago. From the relation between tree growth and stand density given by Figure 16, an estimate was made of the probable stand density under which each of the mature trees must have grown when it was about 35 yrs of age. The estimated past stand densities of the present mature stand were compiled in a histogram (Fig. 23). More than 23% of the trees examined exhibited an early growth pattern comparable to that now shown by trees growing in stands with less than 1000 stems per A. More than half of the present mature stand apparently grew up in stands with fewer than 3000 trees per A at 35 yrs of age.

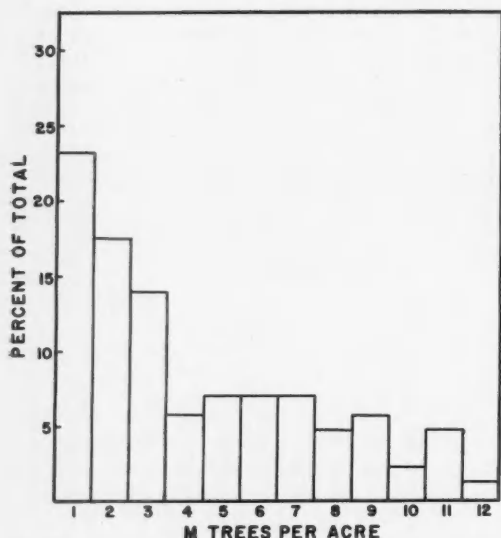


FIG. 23. The early growth of 104 trees from the mature stand at Maverick was used to estimate the stocking density under which these trees may have grown in their early years.

One of several questionable assumptions in this analysis is the conclusion that all of the present mature stand developed from trees that were large dominants in the sapling stands of their youth. Some of the present overstory trees have, on the contrary, rather obviously been more or less suppressed all their lives. It is not uncommon to find 6- or 8-in. trees that are 150 yrs or more old. Several such were included in the Maverick growth analysis. Besides the trees used in the construction of Fig. 23, there were 18 additional trees whose early growth was so small as to indicate that they grew up under a stocking rate far in excess of 15,000 stems per A. This is surely improbable. It is more likely that these 18 trees were small intermediate or codominant trees in their sapling days.

All that Figure 23 suggests with any degree of certainty is that the early growth of a large proportion of the trees that make up the present mature stand was greater than the comparable growth of most saplings today. The implication is very strong that most of the Maverick overstory began its life under conditions of stocking considerably less dense than those found in the area today.

SAPLING STANDS AT MAVERICK AND MALAY GAP

Because of the marked difference in site quality and stand character between Maverick and Malay Gap, it is not legitimate to compare directly the growth of trees on the two areas. Fewer stands were sampled for complete growth data at Malay Gap than at Maverick.

The average growth of the largest trees in the Malay Gap sapling stands is much less than that of trees in stands of comparable density at Maverick.

Measured stem area growth of dominants at Malay Gap is only about two-thirds that predicted from equation (4) and Figure 16. The lower site quality at Malay Gap accounts in part for this difference. More important, though, is the fact that the Maverick growth equation defines growth in sapling stands of wholly different character than those at Malay Gap.

The Maverick equation related growth to stand density in stands whose structure has been determined almost wholly by biological factors of intraspecific competition. These stands have a high proportion of small trees, whereas the fire-thinned stands at Malay Gap tend to have fewer but larger trees. It has been shown (Cooper, in press) that instantaneous growth rates in ponderosa pine stands are more closely related to summed tree diameters per acre than to basal area or to number of trees per acre. This is logical when it is considered that tree diameter is almost directly proportional to the surface area of the cambium.

Because the Malay Gap stands contain fewer very small trees than those of comparable age at Maverick, the summed tree diameters in stands of a given density are greater at Malay Gap than at Maverick. This means that the influence on stand growth of a given number of trees per acre is greater at Malay Gap than in the Maverick stands. Therefore, even aside from site quality, it is to be expected that individual tree growth would be less in stands of a specified density at Malay Gap than at Maverick.

It is likewise not legitimate to compare the total periodic basal area growth per acre of the two sets of stands. The basal area of the Malay Gap stands was sharply but temporarily reduced during the 1948-1957 decade by the fire of 1943. This fact, combined with the known site differences, makes a direct comparison of basal area growth meaningless.

Definite conclusions can, however, be drawn about the diameter distributions and the comparative stand densities in the two areas. The differences in diameter distributions in sapling stands at Maverick and Malay Gap have already been discussed in some detail. Differential removal of smaller stems by fire is plainly the mechanism which produced the Malay Gap diameter distributions. The 1909 stands at Maverick were all exposed to at least one fire early in their lifetime. This fire removed some of the surplus smaller stems, and initiated a change toward a diameter distribution of the type found at Malay Gap. These stands were fully protected after the age of 15, though, while the comparable stands at Malay Gap were being burned twice more. The sapling stands whose distributions are most strongly skewed toward the small trees are those young ones never exposed to fire. Those most strongly skewed toward the large end of the distribution are the Malay Gap and the much older Cooley Mountain stands, all often subjected to surface fires. Intermediate in diameter distribution are the once-burned 1909 stands at Maverick.

Diameter distributions at earlier ten-year intervals were derived for several stands from measurements

of stump sections and increment cores. The shape of the logarithmic basal area histogram changes very little in the interval from about 20 to 50 yrs total age. Variations in shape of the histograms in Figures 8 and 9 seem to be attributable chiefly to environmental factors rather than to normal changes in diameter distribution accompanying stand maturity.

Another striking difference between Maverick and Malay Gap is in the average density of reproduction stands. The comparative figures of Table 6 are probably representative of the difference in the two areas. Nowhere at Malay Gap are there impenetrable pine thickets of the type so common elsewhere (Fig. 24). A reasonable effort was made to include in the sampling program the densest stands observed at Malay Gap. The most densely stocked $\frac{1}{100}$ A that met the other sampling requirements of homogeneity and stand uniformity had the equivalent of 4960 trees per A.



FIG. 24. Closeup of a typical dense thicket at Bog Creek. Cap in foreground gives scale. There is no lack of light on the forest floor even in the densest pine stands.

The lower stand density and the greater relative number of trees in the larger size classes means that the mean growth per tree is greater in the fire-thinned stands at Malay Gap than in stands of comparable age in other areas. The stands at Malay Gap appear more healthy, more open, and are composed of fewer but larger trees than at Maverick (Fig. 25).

It is clearly apparent that reproduction stands are smaller in extent at Malay Gap than elsewhere in the Arizona pine region. Yet, a survey showed that one-fourth of the ground area there was occupied by stands less than 40 yrs of age (Fig. 6). This is surely a normal proportion in a forest of long-lived trees.

THE ORIGIN OF PATTERN AND STRUCTURE

AGE AND DIAMETER STRUCTURE

An important characteristic of the old-growth forests of the White Mountains is their unbalanced age and size class distributions. There is an overabundance of young trees less than 6 in. d.b.h., and many large mature and overmature pines. The inter-



FIG. 25. Pine stand at Malay Gap, partially thinned by recurrent fires. This stand originated in 1914.

mediate age and size classes are obviously deficient.

The missing classes coincide in general with the period of first settlement of the Southwest, and it has been suggested that the early pioneers were responsible for the present lack of intermediate aged stands. It has been reported that the early settlers were particularly careless with fire, or perhaps set fire to the woods deliberately to improve forage conditions. An abnormal increase in the incidence of man-caused fires in the last half of the 19th century is sometimes assigned as the cause of the relative lack of small sawlog trees in the ponderosa pine forest.

The fact that the same unbalanced age distribution occurs in the largely undisturbed forest at Malay Gap argues against this hypothesis. Furthermore, there is little evidence that the early pioneers were particularly free in their use of fire in the woods. Joe Pearce, a long-time resident of Eagar, Arizona, who was employed as the first ranger on the Black Mesa Forest Reserve at the time of its establishment in 1898, reported (personal interview, 1957) that his principle duty in those days was firefighting. He had little trouble enlisting the aid of cattlemen in fighting fire on their own range, for they were constantly apprehensive about the loss of forage. In contrast to the situation in California, there apparently was little organized burning of the woods by white settlers at any time in the last century.

The primary cause for the lack of intermediate aged trees appears to be the infrequent occurrence of the peculiar sequence of weather conditions necessary for establishment of reproduction. There is a large class throughout the White Mountains that apparently dates from about 1839. Most of these 120-yr-old trees are now from 16 to 24 in. d.b.h. There are definite age classes that originated about 1875, about 1890, and possibly in other years; but on the whole there was little regeneration between 1839 and 1909. Many of the present small pole stands started in 1909, and were followed by the extensive 1919 class.

Several older classes can be clearly distinguished. Many trees became established in 1820 and others about 1795. A surprising number of the very large

veterans in the old-growth forest can be dated about 1685.

The importance of the 1919 age class has been stressed repeatedly, and perhaps overemphasized, by many foresters. It is almost wholly lacking in the Maverick area, however. Fire scars on trees in the 1909 pole stands show that the area was burned early in the growing season of 1924, when the 1919 pines were 5 yrs old. If any substantial number of seedlings became established in 1919, they must have been killed by the 1924 fire. It is possible that there was a complete local failure of reproduction at Maverick in 1919. This hypothesis is made plausible by the apparent scarcity of 1919 trees over many square miles, and their relative rarity at Malay Gap. A number of stands that appeared to date from 1919 were sampled, but all turned out to be somewhat younger. Dense pine thickets originating in 1923 and 1928 are as conspicuous in the Maverick region as are the 1919 thickets elsewhere. For the last 25 yrs or so there has been virtually complete failure of pine regeneration throughout the White Mountains.

The age and diameter structure of the forest as a whole is governed by the periodicity of reproduction. A particularly favorable combination of weather conditions has permitted stand regeneration only in occasional years. These waves of reproduction have come at irregular and unpredictable intervals, and have resulted in an irregular and unbalanced forest structure.

PATTERN

The patchwork pattern of the ponderosa pine forest is the expression of a cyclical process of community development, governed by fire and by the intolerant nature of the species. The basic outlines of this process have been presented by Weaver (1943). Watt (1947) has analyzed the theoretical implications of cyclical development in the plant community. It remains to bring these concepts together into a unified hypothesis on the origin and development of pattern in the southwestern pine forest.

The intolerance of ponderosa pine to shade is responsible for the formation of the even-aged groups of which the forest is composed. Even-aged forests are typical of intolerant species in general, for the young trees grow best when not subjected to shade from the mature canopy. The relatively small size of the even-aged groups in the southwestern forest is due to the small size of the openings in which the groups can become established.

As the stand matures, the identity of the groups is maintained by fire. In an opening, a stand of young trees is partially protected by the lack of fuel on the forest floor. In contrast, the ground beneath a group of mature trees is generally covered by a layer of inflammable material. Seedlings that germinate beneath the overstory are rapidly eliminated by the first fire that passes through the stand.

Fire is thus the force that here counteracts the inevitable tendency of plants to take on a random dis-

tribution. Since the seeds of ponderosa pine are widely and more or less uniformly distributed throughout the entire forest, the stand should in time take on a purely random pattern, the pattern of a theoretical all-aged forest with trees of every age occurring in every portion of the stand. Some external influence must be present to overcome the natural tendency for pattern formations to break down and for the vegetation to be distributed randomly. Natural fires impress upon the forest the grouped pattern so characteristic of ponderosa pine, and act to maintain that pattern through time.

Watt (1947) has suggested that most plant communities exhibit a cycle of change divisible into two parts: an upgrade, when the net quantity of plant material is increasing; and a downgrade, characterized by dispersion of material and the breakup of the community. The upgrade portion of the cycle starts slowly, accelerates, and then slows down as the community reaches maturity; the downgrade portion of the curve is precipitous.

A reconstruction of the history of one small area of about $\frac{1}{4}$ A at Maverick illustrates the cyclical pattern of development and breakdown through which the pine forest has passed. This particular quarter-acre is occupied by a dense stand of young pines that originated in 1928. Towering above them are two old veterans, one 34 in. and the other 35 in. d.b.h. Two standing snags, 4 fallen logs, and a burned stump testify that the two big trees are the last survivors of a disintegrating group. Close by in all directions are thrifty pole stands dating from 1909.

The group of large pines, which began to grow about 1715, was apparently still intact in 1909, and then consisted of about 10 mature trees. When the 1909 stands established themselves, seedlings germinated beneath the mature canopy, but grew poorly because of root competition. The first fire that came through the area—in 1924 if not before—killed them all because of their small size and because of the quantity of surface fuel laid down by the overstory pines. Adjacent young stands in openings survived, to produce the thrifty pole stands visible today.

Meantime, the mature stand was starting to break up. One of the old trees must have been dead by 1924, as shown by the burned stump. After maintaining its integrity for more than 200 yrs, the group apparently disintegrated in 20 yrs or less. Interconnection of the root systems by root grafts may have had something to do with the rapid deterioration of the stand once disease or old age got a foothold. With all but 2 or 3 of the former dominant group gone, conditions by 1928 were suitable for reestablishment and survival of a new young stand. The 1924 fire removed most of the surface litter and exposed a good seedbed. There was no longer a heavy needle fall from the mature overstory, nor did the feeble survivors offer intense root competition to the developing young stand. Thus a new cycle was initiated, to repeat itself as before. Under natural

conditions, the new young stand will throughout its life maintain its integrity as a homogeneous even-aged group. Root competition combined with selective removal of small stems by fire will ensure that trees of younger ages cannot successfully become established within the even-aged group.

GROUND COVER VEGETATION

The composition and quantity of the herbaceous ground cover in Southwestern ponderosa pine forests is the result of the interaction of at least three factors: grazing, fire, and the density of the forest canopy. The relationship of fire to ground cover vegetation has been intensively studied in the pine regions of southeastern United States, where prescribed burning is widely employed to control undesirable hardwoods. The situation in the Southwest is somewhat different, for here there is no evident successional trend leading to replacement of pine by other species.

No detailed studies have been made of the effects of fire on subordinate vegetation in the Southwest. Weaver (1951b) concluded that properly conducted prescribed burning does not seriously damage perennial bunchgrass cover under ponderosa pine. In fact, it appears beneficial through partial opening of the reproduction stand and removal of dense needle mats. He considered the same to be true where periodic surface fires have continued.

The herbaceous cover at Malay Gap was the only ground cover vegetation that was analyzed in detail in the present study. The Malay Gap area is especially interesting in that livestock have been virtually excluded, and the ground cover approximates to some degree that of pre-white man days. The district is an important wintering ground for the elk that move down from the high country to the east, so it can by no means be considered entirely ungrazed.

The ground cover at Malay Gap is composed almost wholly of a dense stand of screwleaf muhly (*Muhlenbergia virescens*). A few other grasses and forbs are present, but in most places more than 90% of the volume of herbaceous cover consists of the one species of *Muhlenbergia*. Other species present are *Blepharoneuron tricollepis*, *Sitanion hystrix*, *Panicum bulbosum*, *Stipa pringlei*, *Poa fendleri*, and *Koeleria cristata*. On dry exposed slopes, *Muhlenbergia rigens*, *M. longiligula*, and *Ceanothus fendleri* become more abundant. It is clearly noticeable that forbs of all kinds are much scarcer at Malay Gap than on most comparable sites on the Fort Apache Reservation and adjacent national forests. This difference is almost surely due to differences in grazing history.

The grass cover at Malay Gap is as dense as is to be found anywhere in the southwestern pine zone. Grass production was estimated by harvesting all of the current year's crop within a rectangular wire frame 9.6 sq ft in area. The weight in grams of the grass from one such plot, multiplied by 10, estimates

grass production in lbs per A. The estimated weight of the current year's forage production in openings at Malay Gap was 1620 lbs per A. The standard error of the mean of this estimate is 108.5 lbs. While plant species other than screwleaf muhly were encountered on most of the plots, they occurred in such small quantities that it was impractical to segregate them.

The volume of the herbaceous ground cover is much greater in the open than under the forest canopy (Fig. 26). Ground vegetation was harvested from plots under several degrees of tree cover. Percentage of crown cover was estimated at each sampling point by means of the spherical densiometer described by Lemmon (1956). Seven such points were sampled. Based on 20 separate 9.6 sq ft plots from these 7 points,

$$V = 1600 - 21 C \quad (9)$$

where V is herbaceous cover in pounds per acre and C is percentage of crown cover, expressed as a whole number. The standard deviation of the regression coefficient is 2.5. This equation states that forage production declines about 21 lbs per A for each 1% increase in crown cover. If projected far enough, the equation indicates no herbaceous vegetation at crown densities above about 75%. This is essentially correct, for there is little such vegetation beneath very dense pine stands.



FIG. 26. Grass development in intervals between pine groups at Malay Gap. Note the virtual absence of grass and the accumulation of pine needles beneath the mature group in the background.

No detailed analysis of fire effects on grass cover was made. Observations on the B.S. Gap fire indicate that about 10% to 15% of the grass plants were dead a year following the fire. This fire burned at the very end of the growing season, when grasses were nearly dormant, although screwleaf muhly remains partially green all winter. Dead grass plants were clearly evident in the adjacent unburned area as well, so that many of the dead clumps observed on the B.S. Gap fire might have been due to natural mortality. Few grass seedlings were present. While grass growth was vigorous on the burn, it was noticeably less so than on the adjacent unburned area.

EFFECTS OF FIRE ON SOILS

The effects of fire on soils and on watershed condition have long been a matter of concern. The Annual Report of the Superintendent of the Fort Apache Agency discussed a series of severe fires that took place in the summer of 1904. "These fires were high in the mountains and far from the Agency or Indian homes, and in places almost inaccessible. There was not much damage to the large timber, but the younger growth was almost destroyed. The greatest damage, however, was the burning of the great beds of leaves that conserve or hold the water on the mountain sides. The effect was seen in the great floods that came last winter from the continued rains and the deep snow." (Crouse 1905). Yet, as has already been noted, fires were frequent in the White Mountains for many years before 1904, and accelerated erosion was not severe over most of the area at the turn of the century.

Detailed studies of soil conditions following fire in the White Mountains have been reported elsewhere (Cooper, in press). Under most conditions, a protective layer of duff remained on the forest floor following burning. Soil movement was measurably increased on steep slopes after fire, but the slopes rapidly stabilized and little of the eroded material actually reached stream channels. Soil erosion following light to moderate fires cannot be considered serious on the basalt soils of the White Mountains.

DISCUSSION AND CONCLUSIONS

CHANGES SINCE WHITE SETTLEMENT

The coming of the white man to the Southwest brought many new factors to disturb the ecological balance of the region. Most important were the attempted exclusion of fire from forests and ranges, and introduction of domestic livestock. Both have contributed to changes in the Southwestern pine forests during the last three-quarters of a century, but of the two, protection of the forests from fire has had the greatest effect.

Natural surface fires were the agent which normally thinned young stands of pine reproduction—sometimes too much, sometimes not enough, but on the whole in such a manner as to insure continuous growth of the forest. The pattern of the forest, a pattern of an all-aged stand made up of even-aged groups, was largely maintained by fire.

Fires were started by lightning and by Indians. It is impossible to determine the proportion caused by each. Northern Arizona is an area of extremely high lightning incidence; anthropological studies attest to the role of historic Indians in setting fires. It is likely that prehistoric Indians, who have occupied the region for at least 10,000 yrs, were equally free in their use of fire. It is probable that genetic and evolutionary processes, operating over that length of time, would have brought the ponderosa pine forest into balance with the existing fire regime. The arrival of the Indians may have intensified the extent

of fire in the forest, but lightning fires were prevalent long before.

When the white man brought his cattle and his fire-fighting crews to the Southwest, the forest began to change. Grazing altered both the composition and the quantity of ground cover vegetation. Removal of herbaceous competition and exposure of mineral soil by livestock helped prepare the ground for dense thickets of pine reproduction. Abundant reproduction would have become established in any case, however, for its principal cause was an unusually favorable series of weather conditions.

With few fires to thin dense stands of young pine, they soon grew into almost impenetrable sapling thickets. Man's attempted exclusion of fire without the substitution of some other agent to thin sapling stands and to remove excess fuel has created a condition of near stagnation and of fire hazard that presages no good for the forests of the Southwest.

IMPLICATIONS FOR MANAGEMENT

This study was planned as an investigation of the ecological effects of natural fires in the ponderosa pine forests of Arizona. It was not intended as an evaluation of the controlled burning program being carried out on the Fort Apache Indian Reservation, nor as a study in applied forest management. Nevertheless, no one interested in forest management can avoid drawing some conclusions after intensive effort on a problem of this kind.

Early students suggested that repeated fires were permitting the ponderosa pine forests to produce no more than 40% of their potential growth. It is clear that growth of the primeval pine forests did not reach the maximum potential productivity of the site. Natural fires thinned some sapling stands too severely, and killed an occasional large tree in its prime. Growth surely exceeded 40% of the potential, though; it was perhaps nearer 80%. Under present policies of complete exclusion of fire from most of the forests of the Southwest, growth of young stands has actually declined.

Whether the trend toward excessively dense pine thickets, with their accompanying problems of stagnation, can be reversed and the forest returned to anything like its original condition by the use of prescribed fire is questionable. Forty years of fire protection have perhaps allowed the situation to get beyond control. The pine thickets have grown up to a point that a planned burn is apt either to destroy the whole stand or to do little in the way of needed thinning. It may be that only in newly established stands originating after timber harvest can the silvicultural possibilities of planned fire be fully realized.

Three conclusions seem plain from this study. The first is that some practical and economic means must be found for thinning young pine stands and for reducing the amount of hazardous fuels. At the dense stocking rates characteristic of most of the pine thickets in northern Arizona, virtual stagnation is setting in. The fire hazard is likewise building up

to dangerous levels. The projected pulp industry in Arizona, often held out as a panacea for all the ills of forest management, will do little to remedy the situation. The stands in most urgent need of thinning are those well below pulpwood size. If fire is not to be the tool to do this needed job, some other efficient and inexpensive means must be found to thin the stands and remove surplus fuel.

Secondly, if fire is to be used as a management tool in the ponderosa pine forest, some modifications will have to be made in the present system of marking trees for harvest. The improvement selection method used in the Southwest removes high-risk trees and larger dominants where ever found, favoring the growth of smaller clean-barked trees. If applied over several cutting cycles, this system will eventually convert the forest to a true all-aged condition, with trees of every age on every small unit of the stand. If the natural even-aged group pattern of the forest is thus broken up, it will be impossible to employ fire as a management tool. Seedlings under the cover of a mature tree canopy cannot withstand a fire, natural or planned. Only if the normal group pattern is maintained, permitting seedlings to grow in openings, can reproduction be secured. Some version of the group selection system, now being tested in Idaho ponderosa pine stands (Curtis & Wilson 1958), will be necessary to assure regeneration if fire is to be used as a management tool.

Finally, it must be recognized that small trees in and beneath an even-aged stand are not only not desirable, but are often a positive hindrance to growth. In most cases it is impractical in the Southwest to attempt to establish advance reproduction many years before harvest of the mature stand. The statement of Gaines *et al.* (1958) that in the experimental burns on the Fort Apache Reservation, "Few seedlings less than 3 or 4 feet tall survived on either burned area," is technically accurate but highly misleading. Almost without exception these 3 and 4 ft "seedlings" were no less than 25 yrs old at the time of the fire. Removal of these stunted trees represents a gain to forest management, and not a loss as they imply.

The ponderosa pine forest found by the first white men originated under the influence of fire, and was fully attuned to fire as a part of its natural environment. Forty years of fire exclusion has induced profound and detrimental changes in the growth and structure of the managed forests of the Southwest.

SUMMARY

The late settlement of the region makes northern Arizona particularly suitable for a study of vegetation change resulting from man's use of the land. Changes in the ponderosa pine forests of southwestern United States have been studied through analysis of the historical evidence and of the structure of the present forest stand.

Reports of early visitors indicate that the forest was originally more open than it is today. Dense thickets of young ponderosa pine have covered much

of the region in the last half century. Accompanying the increase in young pines has been a decrease in grass cover and a shift in the botanical composition of the herbaceous vegetation. Accelerated erosion has removed the surface soil layers and induced formation of gullies in some places.

Long term climatic changes do not appear to be a major factor contributing to these changes, nor do the effects of wild animals. Some of the change in herbaceous vegetation is the result of excessive use by domestic livestock, but much is directly due to the increasing density of the pine overstory. Livestock have initiated some of the increase in pine reproduction by reducing grass competition and by exposing a mineral seedbed that makes seedling establishment easier.

The most important change brought about by the white man has been the virtual exclusion of fire from the forests of the Southwest. Under natural conditions, light surface fires, set by lightning or by Indians, burned through all parts of the pine forest at regular intervals of 3 to 10 yrs. These fires acted as natural thinning agents and reduced surplus fuel. The reduction of inflammable grass by grazing animals, and an intensive fire prevention program have largely eliminated fire from the woods. The major cause of the present excess of pine reproduction is exclusion of fire.

Stand structure was studied in two areas typical of the ponderosa pine forests in most of the Southwest, and at the primitive area at Malay Gap, where livestock have been excluded and natural fires have continued. In all the old-growth stands examined, there are fewer trees in the intermediate size classes, from 8 to 20 in. d.b.h., than would be expected from theoretical relations between size classes. There are fewer trees in the age classes from 80 to 120 yrs than expected. In young even-aged stands, diameter distributions are skewed toward the smaller trees in stands never exposed to fire. In stands frequently burned during their development, diameter distributions approach a log-normal form, and conform to theoretical distributions that have been fitted to even-aged stands elsewhere.

Mean growth per tree in even-aged reproduction stands is a linear function of available space per tree. From age 20 to 55 yrs, mean growth per tree in any one stand remains relatively constant from one decade to the next. Apparent stagnation begins as stand density exceeds about 6000 stems per A. 150 to 450 trees per A yield maximum growth per tree. Total basal area growth per acre increases with stand density, then decreases as stocking exceeds 4000 trees per A.

Since competition is mostly for water, not light, the normal suppression pattern characteristic of humid forests does not occur in southwestern ponderosa pine. Small trees continue to grow at a constant slow rate, and suppressed and intermediate trees in the aggregate play a greater role than is usually attributed to them. Natural mortality is low in stands unaffected by fire.

Growth of potential crop trees is a linear function of the logarithm of stand density. Stem area growth of an individual tree is directly proportional to the weight of the current year's needles. Height of dominant saplings is related to stocking and age of stands as well as to site index.

The pattern of mature stands and of reproduction stands was analyzed with a grid of contiguous quadrats. Trees are aggregated into even-aged clumps averaging .16 to .32 A in size. The pattern of reproduction in unburned stands is less distinct than that of the mature stand, or of the reproduction in frequently burned stands at Malay Gap.

The stand at Malay Gap is much more open than that in the unburned area at Maverick, with more grass in the intervals between the trees. The site is not as good at Malay Gap as at Maverick, but the difference in stand conditions is primarily due to the frequent fires which have continued at Malay Gap, and to differences in grazing history. Small saplings are rare beneath the mature canopy at Malay Gap. They have been removed by surface fires supported by fuel dropped by the mature stand. Reproduction at Malay Gap is successful only in openings where there is little fuel. There are many more trees per acre in reproduction stands at Maverick than at Malay Gap. Stocking at Malay Gap, however, is fully adequate to assure a future timber crop.

The effects of a recent natural fire were studied at Malay Gap. Only 18% of the trees less than 1 in. d.b.h. survived the fire. Survival in the 4- to 6-in. class was 84%, and no trees over 8 in. d.b.h. were killed. Natural fires thin sapling stands in three ways: by direct heat damage to the cambium of individual trees, by general raising of the crown level, and by creation of openings around burning logs and stumps. In very young stands, there is rarely enough fuel to carry a fire until the trees are 6 or 8 yrs old. The density of the sapling stand in part regulates the quantity of dry needles and the intensity of the resulting surface fire. Fire thinning of sapling stands is a sort of self-regulating feedback mechanism in which the degree of thinning is governed by stand density.

Analysis of early growth of trees comprising the present mature stand at Maverick showed that their growth in the sapling stage was greater than that of most trees of comparable age in present young stands. The implication is that the older trees began their life in relatively open sapling stands.

The unbalanced size and age class distribution in old-growth stands is due chiefly to the rarity of the peculiar set of weather conditions needed for stand establishment. Trees of only a few distinct age classes are present, and failure of reproduction over a long period in the last century accounts for the relative lack of 8- to 20-in. trees.

The clumped pattern of ponderosa pine is the result of a cyclical pattern of community development, governed by fire and by the intolerant nature of the

species. Fire is the force that counteracts the tendency of trees to take on a random distribution.

The composition and quantity of the herbaceous ground cover is governed by grazing, fire, and the density of the forest canopy. Little serious erosion can be noted following light surface fires.

It is doubtful if, after 40 yrs of protection, use of prescribed fire can now reverse the trend toward excessively dense pine thickets. Silvicultural possibilities of planned fire can probably only be realized in young stands originating after timber harvest. Some practical and economic means must be found for thinning young pine stands and for reducing the amount of hazardous fuel. If fire is to be this means, modifications will have to be made in the present method of marking trees for harvest, which is rapidly converting the even-aged groups into a true all-aged forest. In general, small trees in and beneath an even-aged group are not only not desirable, but are often a hindrance in managed forests.

The ponderosa pine forests of the Southwest evolved under the influence of natural fires. Man's attempted exclusion of fire and introduction of live-stock has induced marked changes in the vegetation of the region.

LITERATURE CITED

- Antevs, E. 1955. Geologic-climatic dating in the West. *Amer. Antiquity* 20: 317-335.
- Arnold, J. F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. *Jour. Forestry* 48: 118-126.
- . 1955. Plant life-form classification and its use in evaluating range condition and trend. *Jour. Range Mgt.* 8: 176-181.
- Bancroft, H. H. 1889. *History of Arizona and New Mexico, 1530-1888*. San Francisco: The History Co.
- Beadle, J. H. 1873. *The undeveloped West, or five years in the Territories*. Philadelphia: National Publ. Co.
- Beale, E. F. 1858. Wagon road from Fort Defiance to the Colorado River. 35 Cong. 1 Sess., Sen. Exec. Doc. 124.
- Bell, W. A. 1870. *New tracks in North America*. 2nd Ed., 2 Vols. London: Chapman & Hall.
- Bent, C. 1851. Letter. In: Report in relation to California and New Mexico. 31 Cong. 1 Sess., Sen. Exec. Doc. 18.
- Bryan, K. 1925. Date of channel trenching (arroyo cutting) in the arid Southwest. *Science* 62: 338-344.
- Byram, G. M. 1958. Some basic thermal processes controlling the effects of fire on living vegetation. *Southeastern Forest Expt. Sta. Res. Note* 114.
- Cable, D. R. 1958. Estimating surface area of ponderosa pine foliage in central Arizona. *Forest Sci.* 4: 45-49.
- Cooper, C. F. (In press). Intraspecific competition and stand growth in even-aged stands of ponderosa pine. *Forest Sci.*
- . (In press). Controlled burning and watershed condition in the White Mountains of Arizona. *Jour. Forestry*.
- Crouse, C. W. 1905. Report of superintendent in charge

- of Fort Apache Agency. Ann. Rept. Dept. Interior, Indian Affairs, Part I: 158-162.
- Curtis, J. D. & A. K. Wilson. 1958. A test of group selection in Idaho ponderosa pine. Jour. Forestry 56: 182-189.
- Darton, H. N. 1925. A resume of Arizona geology. Univ. Ariz. Bull. 119.
- Drake, W. M. 1910. A report on the Coconino National Forest. MS in Winn Collection. Arizona Pioneers Hist. Soc. Library, Tucson.
- Dutton, C. E. 1887. Physical geology of the Grand Cañon district. U. S. Geol. Surv. 2nd Ann. Rept.: 49-166.
- Farish, T. E. 1889. Northern Arizona, its forests, arable, and grazing lands. Phoenix: Ariz. Gazette Printers.
- Fletcher, J. E. & W. Beutner. 1941. Erodibility investigations on soils of upper Gila watershed, Arizona. U. S. Dept. Agr. Tech. Bull. 794.
- Frazier, R. 1885. The Apaches of the White Mountain Reservation, Arizona. Philadelphia: Indian Rights Assoc.
- Gaines, E. M. 1951. A longleaf pine thinning study. Jour. Forestry 49: 790-792.
- Gaines, E. M., H. R. Kallander & J. A. Wagner. 1958. Controlled burning in southwestern ponderosa pine: Results from the Blue Mountain plots, Fort Apache Indian Reservation. Jour. Forestry 56: 323-327.
- Grieg-Smith, P. 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. Ann. Bot. 16: 293-316.
- Hack, J. T. 1942. The changing physical environment of the Hopi Indians of Arizona. Peabody Mus. Papers, Harvard Univ., Vol. 35, No. 1.
- Hakluyt, R. 1600. The principal voiaiges, traffiques, and discoueries of the English nation . . . Ed. 1600, Vol. 3. London.
- Haskett, B. 1936. History of the sheep industry in Arizona. Ariz. Hist. Rev. 7(3): 3-49.
- Holsinger, S. J. 1902. The boundary line between the desert and the forest. Forestry & Irrigation 8: 21-27.
- Hughes, L. C. 1893. Report of Governor of Arizona to Secretary of Interior. In: Ann. Rept. Dept. Interior, Misc. Repts., 1893.
- Ives, J. C. 1861. Report upon the Colorado River of the West, explored in 1857 and 1858. 36 Cong. 1 Sess., House Exec. Doc. 90.
- Jones, E. W. 1945. The structure and reproduction of the virgin forests of the north temperate zone. New Phytol. 44: 130-148.
- Kearney, T. H. & R. H. Peebles. 1951. Arizona flora. Berkeley & Los Angeles: Univ. Calif. Press.
- Keith, J. O. 1956. The Abert squirrel (*Sciurus aberti aberti*) and its relationship to the forests of Arizona. Unpub. M.S. Thesis, Univ. Arizona Library.
- Koyama, H. & T. Kira. 1956. Intraspecific competition among higher plants. VIII. Frequency distribution of individual plant weights as affected by the interaction between plants. Inst. Polytech. Osaka City Univ. Jour. 7(D): 73-94.
- Lavin, F. & H. W. Springfield. 1955. Seeding in the southwestern pine zone for forage improvement and soil protection. U. S. Dept. Agr. Handbook 89.
- Leiberg, J. B., T. F. Rixon & A. Dowell. 1904. Forest conditions in the San Francisco Mountains Forest Reserve, Arizona. U. S. Geol. Surv. Prof. Paper 22.
- Leemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Sci. 2: 314-320.
- Leopold, A. 1921. A plea for recognition of artificial works in forest erosion control policy. Jour. Forestry 19: 267-273.
- Lynch, D. W. 1958. Effects of stocking on site measurement and yield of second-growth ponderosa pine in the Inland Empire. Intermountain For. & Range Expt. Sta. Res. Pap. 56.
- . 1959. Effects of a wildfire on mortality and growth of young ponderosa pine trees. Intermountain For. & Range Expt. Sta. Res. Note 55.
- McDonald, J. E. 1956. Variability of precipitation in an arid region: A survey of characteristics for Arizona. Univ. Ariz. Inst. Atmos. Physics Tech. Rept. 1.
- McHenry, D. E. 1935. Quaking aspen: Its future in the park. Grand Canyon Nature Notes 9: 361-365.
- Maguire, W. P. 1956. Are ponderosa pine cone crops predictable? Jour. Forestry 54: 778-779.
- Merriam, C. H. 1890. Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado, Arizona. U. S. Dept. Agr. North Amer. Fauna 3.
- Meyer, H. A. & D. D. Stevenson. 1943. Structure and growth of virgin beech-birch-maple-hemlock forests in northern Pennsylvania. Jour. Agr. Res. 67: 465-484.
- Meyer, W. H. 1930. Diameter distribution series in even-aged forest stands. Yale Univ. School Forestry Bull. 28.
- Morris, W. G. & E. L. Mowat. 1958. Some effects of thinning a ponderosa pine thicket with a prescribed fire. Jour. Forestry 56: 203-209.
- Nelson, E. W. 1884. Explorations in southern Arizona. Smithsn. Inst. Ann. Rept. 1884: 20-24.
- Ogle, R. H. 1940. Federal control of the Western Apaches, 1848-86. Albuquerque: New Mex. Hist. Soc.
- Pattie, J. O. 1905. Personal narrative of James O. Pattie of Kentucky. Ed. 1831 by Timothy Flint. New Ed., R. G. Thwaites. Cleveland: Arthur H. Clark Co.
- Pearson, G. A. 1910. Reproduction of western yellow pine in the Southwest. U. S. Dept. Agr. Forest Serv. Circ. 174.
- . 1923. Natural reproduction of western yellow pine in the Southwest. U. S. Dept. Agr. Bull. 1105.
- . 1942. Herbaceous vegetation a factor in natural regeneration of ponderosa pine in the Southwest. Ecol. Monog. 12: 313-338.
- . 1950. Management of ponderosa pine in the Southwest. U. S. Dept. Agr., Agr. Monog. 6.
- Plummer, F. G. 1904. Forest conditions in the Black Mesa Forest Reserve, Arizona. U. S. Geol. Surv. Prof. Paper 23.
- Powell, J. W. 1879. Report on the lands of the Arid Region of the United States, with a more detailed account of the lands of Utah. 2nd. Ed. U. S. Geograph. & Geol. Surv. Rocky Mt. Region. Washington: Govt. Printing Off.
- Prodan, M. 1952. Die Verteilung des Vorrates gleichaltriger Hochwaldbestände auf Durchmesserstufen. Forst- und Jagdzeit. 124: 93-106.

- Rasmussen, D. I. 1941. Biotic communities of Kaibab Plateau, Arizona. *Ecol. Monog.* 11: 229-276.
- Rixon, T. F. 1905. Forest conditions in the Gila River Forest Reserve, New Mexico. U. S. Geol. Surv. Prof. Paper 39.
- Rothrock, J. T. 1875. Preliminary botanical report, with remarks upon the general topography of the region traversed in New Mexico and Arizona; its climatology, forage plants, timber, irrigation, sanitary conditions, etc. *Geogr. Expl. Surv. West of 100th Merid.*, Ann. Rept. Chief Engin., War Dept., 1875, Append. LL.
- . 1878. Report upon the botanical collections made in portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona during the years 1871-1875. In: Wheeler, G. M., Rept. U. S. Geogr. Surv. West of 100th Merid. 6: 3-297.
- Rummel, R. S. 1951. Some effects of livestock grazing on ponderosa pine forests in central Washington. *Ecology* 32: 594-607.
- Schaefer, V. J. 1957. The relationship of jet streams to forest wildfires. *Jour. Forestry* 55: 419-425.
- Schulman, E. 1956. Dendroclimatic changes in semi-arid America. Tucson: Univ. Ariz. Press.
- Show, S. B. & E. I. Kotok. 1924. The role of fire in the California pine forests. U. S. Dept. Agr. Bull. 1294.
- Simpson, J. H. 1850. Report of an expedition into the Navajo country. 31 Cong. 1 Sess., Sen. Exec. Doc. 64.
- Snedecor, G. W. 1956. Statistical methods, 5th Ed. Ames: Iowa State Coll. Press.
- Stevenson, J. J. 1881. Report upon geological examinations in southern Colorado and northern New Mexico, during years 1878 and 1879. U. S. Geogr. Surv. West of 100th Merid., Vol. 3 (Supp.).
- Sudworth, G. B. 1900. Stanislaus and Lake Tahoe Forest Reserves and adjacent territory. U. S. Geol. Surv. 21st Ann. Rept., Pt. 5: 499-562.
- Taylor, W. P. & D. M. Gorsuch. 1932. A test of some rodent and bird influences on western yellow pine reproduction at Fort Valley, Flagstaff, Arizona. *Jour. Mammal.* 13: 218-223.
- Thompson, H. R. 1958. The statistical study of plant distribution using a grid of quadrats. *Austral. Jour. Bot.* 6: 322-342.
- [Thornber, J. J.?] 1905. Report of trip across the San Carlos and White Mountain Indian Reservation, July 18 to 29, inclusive. MS in: Range conditions in Arizona, 1900-1909. Misc. Coll., Univ. Ariz. Library.
- U. S. Dept. Agriculture. 1910. Annual Report. Washington: Govt. Printing Off.
- Watt, A. S. 1947. Pattern and process in the plant community. *Jour. Ecol.* 35: 1-22.
- Weaver, H. 1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific slope. *Jour. Forestry* 41: 7-14.
- . 1947. Fire—Nature's thinning agent in ponderosa pine. *Jour. Forestry* 45: 437-444.
- . 1951a. Fire as an ecological factor in the southwestern ponderosa pine forests. *Jour. Forestry* 49: 93-98.
- . 1951b. Observed effects of burning on perennial grasses in the ponderosa pine forests. *Jour. Forestry* 49: 267-271.
- . 1955. Fire as an enemy, friend, and tool in forest management. *Jour. Forestry* 53: 499-504.
- . 1959. Ecological changes in the ponderosa pine forest of the Warm Springs Indian Reservation in Oregon. *Jour. Forestry* 57: 15-20.
- Webb, S. F. 1900. Report to the Salt River Valley Water Supply Protective Assn. MS in: Range conditions in Arizona, 1900-1909. Misc. Coll., Univ. Ariz. Library.
- Webb, W. P. 1931. The Great Plains. Boston: Ginn & Co.
- Wheeler, G. M. 1878. Report upon United States Geographical Surveys West of the 100th Meridian. Vol. 1, Topography. Washington: Govt. Printing Off.
- Whipple, A. W. 1856. Report of explorations for a railway route near the thirty-fifth parallel of north latitude, from the Mississippi River to the Pacific Ocean. Pacific Railroad Repts., Vol. 3. 33 Cong. 2 Sess., House Exec. Doc. 91.
- Winship, G. P. 1896. The Coronado expedition, 1540-1542. *Bur. Amer. Ethnology* 14th Ann. Rept., Part I: 329-637.
- Yli-Vakkuri, P. 1954. Tutkimuksia puiden välisistä elemellisistä juuriyhteisistä mannikoissa [Studies on root grafts in pine stands]. *Acta Forest. Fenn.* 60(3): 1-117.

ASPECTS OF THE ECOLOGY OF THE CALIFORNIA PEBBLE CRABS (CRUSTACEA: XANTHIDAE)

JENS W. KNUDSEN

Department of Biology, Pacific Lutheran College, Parkland, Washington

TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION AND ACKNOWLEDGMENTS	165	HABITS AND BEHAVIOR	172
MATERIAL	165	Locomotion and Pereiopod Adaptations	172
The Family Xanthidae, Alcock	165	Freeze Response and Aufbaumreflex	173
<i>Lophopanopeus leucomanus leucomanus</i>		Catalepsy-like Response	175
(Lockington)	166	Visual, Chemical, and Tactile Senses	175
<i>Lophopanopeus bellus diegensis</i> Rathbun	166	Food and Feeding Habits	180
<i>Paraxanthias taylori</i> (Stimpson)	166	PREDATORS, PARASITES, AND COMMENSALS	181
<i>Cycloxanthops novemdentatus</i> (Lockington)	167	Predators	181
HABITAT OF THE CALIFORNIA XANTHIDAE	167	Parasites	181
Site of Studies	167	Commensals	182
Physical and Ecological Aspects of		ECONOMIC AND FUTURE STATUS OF THE	
the Habitat	167	XANTHIDAE OF CALIFORNIA	183
Generic Specificity of Habitat	171	SUMMARY	183
		LITERATURE CITED	184

INTRODUCTION AND ACKNOWLEDGMENTS

The present study is concerned with the natural history of the more common members of the California Xanthidae, the pebble crabs. These secretive individuals are common, but seldom seen, members of the lower intertidal-zone fauna, found along the protected rocky coasts of California. Their superficial resemblance to beach pebbles along with their ability to hide and "play dead" make them an interesting group to study. Because of their similarity in behavior, the scope of this paper has been broadened to cover the four major species found locally, rather than just one species. Thus, *Lophopanopeus leucomanus leucomanus* (Lockington), *Lophopanopeus bellus diegensis* Rathbun, *Paraxanthias taylori* (Stimpson), and *Cycloxanthops novemdentatus* (Lockington) are discussed collectively as the major California Xanthidae, where the data applies to all four species, or individually, when they differ from one another. Whenever possible additional material concerning the less common members of the California Xanthidae is added for comparison.

The emphasis of this paper has been placed on a description of the basic habitats occupied by the Xanthidae and of such habits of the pebble crabs as shed light on their natural history. The physical and oceanographic aspects of the habitat areas, together with the fauna and flora, were studied extensively in the field. The habits and behavior of the xanthid crabs were studied both in the field and in laboratory aquaria. Too frequently ecological papers dealing with intertidal animals present only such activities as are observed during low tide. As the animal lives in the quiet tidepools only a fraction of

the time, these papers fail to give a full account of the life habits. This was overcome to some degree by anchoring an innertube raft over the habitat at high and intermediate tides and observing crab activities with the aid of a snorkel-tube and face plate. The writer was able to spend more than thirty hours in this type of observation.

The laboratory research and study of preserved specimens was done at the Allan Hancock Foundation of the University of Southern California. Field work centered at Palos Verdes, California, but was conducted from Oregon to the Gulf of California and the Mexican mainland.

The writer is deeply grateful to Dr. Norman T. Mattox and Dr. John S. Garth for their assistance and guidance in this study. He also wishes to thank Dr. E. Yale Dawson for identifying algal fragments recovered during stomach-content investigations; Dr. Paul L. Horner, Scripps Institution of Oceanography, for two weeks at Visciano Bay, Baja California, Mexico aboard the "M. V. Horizon"; the California Department of Fish and Game for five weeks in the Gulf of California aboard the "M. V. Yellowfin"; Mr. Patric L. Doheny for two weeks off the Mexican mainland below Baja California; and Captain G. Allan Hancock for the privilege of special collecting in connection with this paper from the "Velero IV," and for laboratory space in the Allan Hancock Foundation.

MATERIAL

THE FAMILY XANTHIDAE, ALCOCK

Members of the Family Xanthidae along the west coast of the Americas are typically found in tropical

and sub-tropical waters. Garth (1946), who has made the most complete survey of the littoral Brachyura of the Galapagos Archipelago, lists 25 genera and 42 species of xanthid crabs there. In comparison with this, there are only 5 genera and 7 species found along the southern half of the California Coast, and 2 of these species are found north of San Francisco Bay. Therefore, in this paper, the California Xanthidae are considered as a displaced part of a warm water fauna. The major genera and species dealt with in this paper will be discussed briefly.

LOPHOPANOPEUS LEUCOMANUS LEUCOMANUS
(Lockington)

Mature members of the genus *Lophopanopeus* are smaller in size than specimens of the other genera treated herein. *Lophopanopeus l. leucomanus* is easily distinguished from related forms by the lack of pubescence on the dorsal surface of the carapace and the carpus and propodus of the walking legs. (Fig. 1). The carpus of the chelae bear reticulating ridges and pits. Immature individuals are quite variable in coloration. Ground colors of the carapace commonly found are tan, light brown, dark brown, orange, red-orange, and magenta, with markings of light or dark brown. The pattern of marking varies with the individual, or may be lacking. Areas of marking most frequently found are the mesogastric and metagastric regions, and the places of ligament attachments under the carapace. The ground color is most vivid after ecdysis, but becomes darker and duller with time. The legs and under-parts are usually white, tan, or light brown. Mature individuals are generally of uniform shades of tan or brown. This subspecies ranges from Monterey Bay, California, in the north to Rosarito Beach, Baja California, Mexico (Menzies 1948: 12).

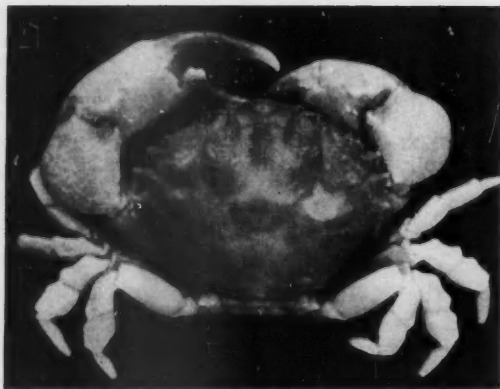


FIG. 1. *Lophopanopeus l. leucomanus*.

LOPHOPANOPEUS BELLUS DIEGENSIS Rathbun

This subspecies bears pubescence on the carapace and proximal segments of the ambulatory legs and has irregular lumps on the carpus of the chelae (Fig. 2). The color is typical of the other member of this genus

discussed above. Immature specimens are generally multicolored, with ground colors of tan, light brown, dark brown, orange, and red-orange. Mature specimens are of dull, light brown to dark, olive-brown colors. The present writer takes exception to Rathbun (1930: 328), who states this species is "never conspicuously marked." Distribution ranges from Monterey Bay, California, in the north to Mission Bay, San Diego, California, in the south (Menzies 1949: 9). The writer has examined additional specimens from Rosarito Beach, Baja California, Mexico.

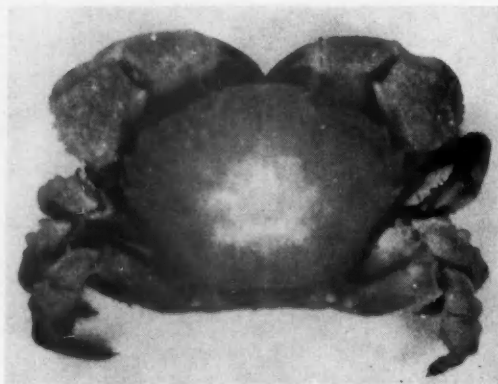


FIG. 2. *Lophopanopeus bellus diegensis*.

PARAXANTHIAS TAYLORI (Stimpson)

Mature members of this species are much larger than those of *Lophopanopeus* (Fig. 3). They are distinguished by a subhexagonal, areolated carapace and hairy legs. The color in life is a uniform dark red in younger animals to a purple color in older animals. The underparts are lighter in color. The "fingers" are black. This is the only major species of California Xanthidae which has a uniform coloring in the juvenile stage. The zoea and first crab stages are red as are the larger, mature specimens. This species is found from Monterey Bay, California, to Magdalena Bay, Baja California, Mexico (Rathbun 1930: 467).

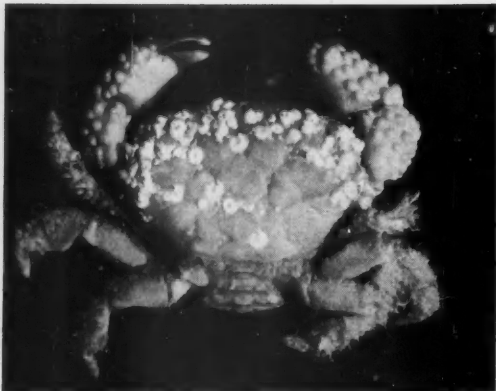


FIG. 3. *Paraxanthias taylora*.

CYCLOXANTHOPS NOVEMENTATUS (Lockington)

The nine-toothed carapace of this, the largest of the California Xanthidae, separates it from the other genera and species (Fig. 4). The small immature stages of this species, like those of the genus *Lophopanopeus*, are variable in coloration. Common ground colors are off-white, tan, red-brown, gray, gray-brown, gray-red, orange, and dark brown. The ground color is often overshadowed by complex marking of a darker or (generally) lighter color. The markings of an individual are retained from molt to molt, but the colors frequently go through drastic changes, i.e.,—pre-molt red-orange, and a post-molt gray-brown. The markings become less vivid with age. In the size classes of 19.0 mm wide to 26.0 mm wide, the color becomes a uniform red-brown which is typical of young mature animals. Just after ecdysis these animals are of a scarlet color, but turn to red-brown on the body and black on the claws in a few weeks' time. Very large, old individuals are red-brown after ecdysis but turn a dark purple in a few weeks' time. When rubber tubing was placed over the claws of newly molted crabs the covered area was prevented from turning color, while the areas on each side of the rubber turned black or dark purple.

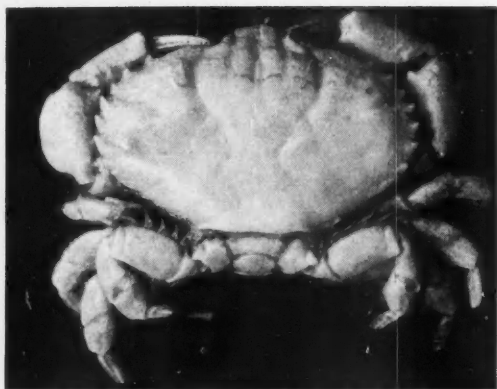


Fig. 4. *Cycloxanthops novementatus*.

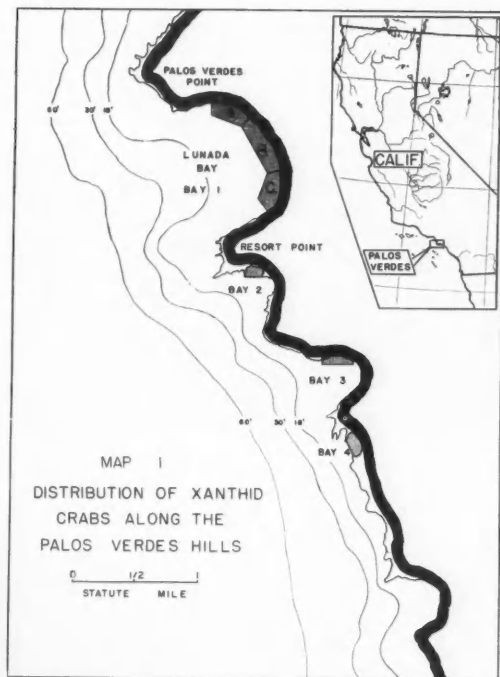
This species ranges from Monterey Bay, California, to Guadalupe Island, Baja California, Mexico (Rathbun 1930: 293). Specimens deposited in the Allan Hancock Foundation extend this range to Abasco Point, Baja California, Mexico.

HABITAT OF THE CALIFORNIA XANTHIDAE

SITE OF STUDIES

Sites for study were chosen on the basis of population densities after a careful search of the coast north and south of Los Angeles had been made. Excellent areas for investigation were found in a series of four small bays (see Map 1) along the Palos Verdes Hills. These sites were visited during nearly every series of low tides for more than one year. Another xanthid habitat with conditions different from those at Palos Verdes was located at Corona del Mar, but this site,

being small and less complex, was not visited as frequently.



The ecological data presented are the results of observations made in the study areas and in other more remote areas which were visited only a few times. In California collections and observations were made at Monterey Bay, Carmel, Santa Cruz Island, Santa Catalina Island, La Jolla, and San Diego. The writer also collected at Boiler Bay, Oregon; at Viscaino Bay, Baja California, on the Pacific and Gulf side of the southern part of Baja California, the Tres Marias Islands, and the Mexican mainland. Field data have been corroborated by laboratory observations and experiments whenever possible.

PHYSICAL AND ECOLOGICAL ASPECTS OF THE HABITAT

Several different xanthid habitats have been found which are inhabited by two or more genera of juvenile or adult crabs. For simplicity, therefore, the basic habitat types will first be described as physical and ecological units, and then the micro-habitat occupied by each species within these units will be given.

Habitat One. Bays Two and Four. (Fig. 5). A survey made of the habitats of *Paraxanthias taylori* and *Cycloxanthops novementatus* along the Palos Verdes shore (Map 1, Bay 1—A, Bay 2, Bay 3, and Bay 4) reveals that these areas are constant in relation to existing oceanographic conditions. Few crabs of these species are found in other parts of the bays which also have an adequate rocky substrate. Furthermore, the fauna and flora of the habitat areas differ from those of the surrounding bay. Obviously these

areas of high crab population approach optimum conditions for successful crab survival and reproduction, while the beaches a few hundred yards away do not. Bays Two and Four are perhaps the best examples and will be used to describe this type of habitat. They are, physically, very much like other xanthid habitats, such as the area north of the La Jolla Caves, California.



FIG. 5. Aerial view of the primary habitat area along the cliffs of the Palos Verdes Hills, California, where the major part of the research was conducted. Lunada Bay is on the left, Resort Point center, and "Bay Two" to the right of Resort Point (see Map I). Aerial photo by Dr. K. O. Emery.

Geologically, the habitats consist of very large tidepools at the base of steep cliffs along the Palos Verdes Hills (Fig. 5). They typically have a substrate of coarse, shelly sand and gravel which is overlain with 2-3 ft of large, rough, cherty-limestone boulders. These boulders are cemented together by colonies of tube snails (*Aletes squamigerus*), encrusting Bryozoa (*Eurystomella* sp.), and crustose red algae (*Lithothamnion* and other genera). The rough contours of the boulders and the relation of one boulder to another have created innumerable inter-rock spaces. These often adjoin to form an anastomosis of small spaces and tunnels.

The "tidepools" are separated from the outer bay by a continuous sand and rock bar or reef, or by discontinuous boulders. These are submerged at high and intermediate tides, but are partly or totally exposed at low tides. At the La Jolla Cave area the rocky reef is exposed only at extreme low water, but forms a large, deep pool behind it. Apparently it is the reef-like function of the rock formation which sets these habitat areas apart from the adjacent coastline.

The major wave-fronts observed from Resort Point were from the west and southwest. As each wave-front shoaled into the bays, the ground friction abreast of each rocky point caused refraction and consequent bending of the wave-front until the shore or a line of equal friction was reached. If lines of equal energy are placed at right angles to a westerly wave-front, and these, in turn, are corrected to fit the bottom topography, it may become evident that five units of the energy is spent on the rocky points for each unit of energy which strikes the habitat area. The unit ratio of energy becomes greater with south-

westerly waves and smaller with waves of northern origin. This reduction of energy permits a protected rocky-beach situation on an otherwise exposed rocky coast.

These areas are further protected by the reefs which lie more or less parallel to the approaching wave fronts. Fig. 6 shows the large tidepool (about 180×200 ft) in Bay two with a double chain of rocks barring its entrance. Upon close examination it was seen that the abruptly rising substrate and rocky reef caused the existing long waves to break. When past the reef zone, and upon reaching the somewhat deeper water of the tidepool, the waves reformed to long waves of the original period but with reduced velocity and length. Friction from the boulder substrate and kelp beds further reduced the wave strength. Upon reaching the inland side of the tidepool the waves again broke. With the change of the tide level the level of wave attack also changed. Waves were noticeably reduced in velocity at mean-high tide, and at high tide some wave translation over the reef was still noticed.



FIG. 6. A large tidepool (Habitat One) in "Bay Two" as seen during a minus tide. Note the chain of large rocks on the outer side of the pool which protect this habitat from wave action.

By watching (while under water) the sea hare (*Aplysia californica* Cooper) secrete its ink, one could see the rotation of water beneath the wave crest. When trough-like spaces between the boulders occurred at right angles to the wave front the horizontal motion of water was continuous to the existing depth of the trough. However, when troughs were parallel to the wave front, or when inter-rock pockets occurred, the horizontal water action was greatly reduced at the pool depth. This offers quieter feeding grounds for the tidepool animals at higher tide periods, and affords more protection for newly spawned larvae.

There are many favorable oceanographic and ecological conditions created by the reef action besides the reduction in wave velocity. Sea water entering the area is first aerated as the wave breaks upon the reef, and secondly when it reaches land. Thus the oxygen content is potentially high at all times (7.3 ppm). At low tide there is still ample water ex-

change so that the water never has time to stagnate. The horizontal water motion is adequate, on the other hand, (1) to prevent waste accumulation between the boulders of the substrate, (2) to remove excretory products, and (3) to prevent hydrogen sulfide formation. Hydrogen sulfide mud was never encountered beneath boulders in this area. At low tide periods a gradual heating may occur with the receding of the tide. The range of temperature increase due to insolation and reduced water exchange varied from 1° to 4° F. Also a slight decrease of 0.06% salinity was recorded in Bay Two, perhaps due to a slight inflow of ground water.

Frequently low tides leave the xanthid habitat exposed and the crabs, as well as other members of the biota, are left to wait for the returning tide. A study of the time of low tide in relation to the seasons reveals that low water occurs during daylight hours in the colder months of the year when the temperature is low and the humidity relatively high. At such times tidepool heating by insolation is beneficial to the inhabitants. On the other hand, during the warm summer months low tides occur during the night or early daylight hours when the humidity is also relatively high and the air temperature is at its lower daily limit. Excessive tidepool heating does not occur at these times. Thus it can be seen that the time of the daily low tide is favorable at this latitude and that the fauna and flora are not readily subjected to overheating or dessiccation.

The algal components of this habitat are many and varied. With the change in seasons many species produce a rich growth while others are reduced to a more-or-less dormant, stoloniferous form. Some species which are always present serve as indicators of the specific area within the tidepool where xanthid crabs will be found.

Below the zone of *Pelvetia fastigiata* (J. Agardh) De Toni, at about the 1 ft 5 in. tide level, the rocks are covered with an algal turf composed of the following species: *Ceranium* sp., *Ectocarpus cylindricus* S. and G., *Gigartina spinosa* (Kutzing) Harvey, *Gigartina gracilis* Lamouroux, and *Ulva lobata* (Kutzing) S. and G. This turf contains much sand as well as algal rhizoids and appears as a thick mossy layer above the rocks.

Beginning at about the 0.05 ft tidal level the turf on the exposed rocks changes in nature and is composed of the following dominant species: *Colpomenia sinuosa* (Roth) Derbes and Solier, *Corallina gracilis* Lamouroux, *Bossia orbigniana* (DeCaisne) Manza, *Bossia gardneri* Manza, *Ulva lobata* (Kutzing) S. and G., *Lithophyllum* spp., *Lithothamnium* sp., *Hildebrandia occidentalis* Setchell, and *Petrocelis* sp. Except for the crustose algae these species form a dense, erect turf 3-5 cm high. Other species which also occur seasonally on the sides or tops of these rocks are: *Dictyopteris zonarioides* Farlow, *Rhodoglossum affine* (Harvey) Kylin, *Zonaria farlowii* S. and G., *Dictyota binghamiae* J. Agardh, *Zanardinula linearis* (Kylin) Papenfuss, *Gelidium pursillum* (Stackhouse)

Le Jolis, *Gelidium coulteri* Harvey, *Lorensia* sp., *Phyllospadix scouleri* Hooker, *Pterocladia pyramidale* (Gardner) Dawson, *Acrosorium uncinatum* (J. Agardh) Kylin, *Cladophora microcladioides* Collins, and *Cystoseira osmundacea* (Menzies) C. Agardh. On the in-reef side of the pool, where a deep bottom of sand and rock occurs, the following species are often present: *Phyllospadix scouleri* Hooker, *Porphyra naiadum* Anderson, *Egregia laevigata* Setchell, and *Sargassum agardhianum* Farlow.

The erect coralline and *Colpomenia* turf serves as a good indicator of this type of xanthid habitat. Many additional species of algae which have not been mentioned occur in this area, but these have not proved significant to this study.

Many animals in this habitat are in some way associated with the xanthid crabs and will be discussed under various topics throughout this paper. However, several animals are important in that they help create or modify the xanthid niche. The function of cementing rocks together, performed by tube snails, bryozoans, and some crusting algae, has already been mentioned. The tube snail, *Aletes squamigerus*, also forms twisted masses of intertwined tubes beneath the rocks. These masses leave thousands of small spaces where crabs may hide. Several sponges, such as *Verongia thiona*, *Leucosolenia eleanor*, *Leuconia heathi*, and *Rhabdodermella nuttingi*, partly fill the inter-rock spaces and create many suitable hiding places. Several species of sessile pelecypods, tunicates, and annelids also serve the same function.

This type of biotope includes all the factors required by the xanthid species which inhabit the coral-head and rock habitat prevalent in tropical Pacific waters: a solid substrate, a reticulum of small spaces in which to hide or to move about to feed, ample microscopic algae for food, protection from predators and wave action, and a constant exchange of fresh, aerated water. The physical unit found in the coral head is replaced by cemented rock, worm-tube masses, bryozoa, and sponges in a typical, but slightly coarser, fashion. Temperature conditions of the northern complex differ from those of tropical waters to some degree, and would be a limiting factor for southern genera if introduced in the north. Aside from this, however, the oceanographic and physical feature of Habitats One and Two are remarkably like those of tropical xanthid zones. These similarities make the northern displacement of members of an otherwise warm-water fauna less difficult to understand.

Habitat Two. Lunada Bay, "B" and "C". Geologically this habitat is similar to Habitat One in that it lies along the steep cliffs of the Palos Verdes Hills. As seen in Map 1 the habitat lies at the head and at the south end of the bay. The floor of this area consists of a very flat shelf across the back of the bay. Bay One, "B", consists of a coarse sand substrate covered with large, generally flat, slabs of chert rock. These are seldom more than one layer deep. Bay One, "C", consists of a coarse sand substrate which is divided by ridges of protruding rock.

and with some loose rock, either piled on the ridges, or lying directly on the sand. At low tide a continuous series of large tidepools is left between the rocky ridges.

The wave action directed into this habitat is altered by several physical factors. First, there is some refraction of waves which pass by Resort Point due to bottom friction. Secondly, the flat shelf causes larger waves to break and re-form, resulting in a reduced length and velocity. Thirdly, large boulders which are irregularly situated on the seaward side of the shelf tend to further disrupt the wave formation and reduce wave velocity. With bad weather the wave action tends to become more violent in this habitat than in the preceding one. The water occasionally becomes muddy and cluttered with loosened sea weed.

Algal components of this habitat are fewer in number than in Habitat One. A good indicator of this area is the dense *Gigartina* turf which is composed of the following species: *Gigartina boryi* S. and G., *Gigartina spinosa* (Kützinger) Harvey, and *Gigartina canaliculata* Harvey. The following crustacean algae are also common: *Petrospongia rugosum* (Okamura) S. and G., *Ralfsia hesperia* S. and G., *Lithothamnium* sp., and *Hildenbrandia occidentalis* Setchell.

Several species of algae and one species of marine grass are washed into this habitat from deeper water and are deposited on the beach or under large rocks. These are important, for xanthid crabs frequently tunnel into such a deposit and reside there. Larger xanthid crabs also use it as food after going through ecdysis. The following species were found to be most common: *Gelidium purpurascens* Gardner, *Gelidium coulteri* Harvey, *Porphyra naiadum* Anderson, *Microcladia coulteri* Harvey, and *Phyllospadix scouleri* Hooker.

The entwining mass of tubes formed by the snail, *Aletes squamigerus*, is important in this habitat in that it forms additional hiding space for xanthid crabs. Much of the loose surface rock was pitted at one time by the action of anemones and sea urchins. When these pitted surfaces face the substrate they also create innumerable residing places for marine animals. The ghost shrimp, *Callinassa affinis*, forms its burrows under these surface rocks, but no xanthid crabs were ever found to reside within them.

This habitat is also a substitute for a major xanthid zone of tropical Pacific waters which supports several genera of crabs. This tropical complex is found inshore of large coral reefs where rock or dead coral heads overlie the coarse sand. The xanthid crabs are found under the rock at about the +6 in. tide level or within the coral-head mass (similar to the tube snail mass of California). The wave action is also reduced in the tropical waters by reefs as it is in the north by boulders. Other requirements such as food, fresh circulating water, and protection from waves and predators are supplied in identical fashion in both areas.

Habitat Three, Newport Channel, Corona Del Mar.

This habitat area is located on the Corona Del Mar side of the Newport Channel between the cable crossing and the Kerekhoff Marine Laboratory. The xanthid members of this habitat live exclusively in association with the large boulders (Fig. 7) which form the bank of the canal. In some areas smaller rocks have slipped into the canal and lie upon the otherwise flat, coarse-sand substrate.



FIG. 7. Another xanthid-crab habitat (Habitat Three) inside the Newport Channel at Corona Del Mar, California, as seen during low tide. Crabs hide beneath loose rocks or in the tube-snail masses on the channel wall at the right.

Waves in this area are not of oceanic origin but are created by local winds or passing ships. They are small in most instances and break directly upon the sand at low tide or upon the channel wall at high tide. Of greater importance than wave action are the currents which pass the area. Water is almost constantly running in or out of the channel to maintain the state of sea level dictated by the tide. Factors which tend to regulate or reduce the current velocity at the habitat site are (1) the magnitude of tidal change and (2) the frictional resistance at the rocky channel walls and shallow sandy floor of the channel's edge.

The chief rock weed here is *Gigartina canaliculata* which covers the rocks on the wall and floor of the channel. Additional species which appear seasonally are: *Corallina gracilis* Lamouroux, *Gelidium coulteri* Harvey, *Dictyopteris zonarioides* Farlow and *Egregia laevigata* Setchell.

The most important animal in this habitat is again the tube snail, *Aletes squamigerus*. With reduced wave action this animal is able to build its tube with a minimum of support. The number of animals is also so great that masses of interlacing tubes form layers three to six inches thick along the rock wall and floor of the channel. Microscopic algae, hydroids, sponges, anemones, and many mollusks also dwell within the tube mass, and tend to strengthen the structure.

Physically this habitat is similar to Habitats One and Two as far as the xanthid requirements are concerned. The tube snail niche on the channel sides substitutes for the upper layers of rock in Habitat One and is occupied by *Paraxanthias taylora*. The

rock over-lying the sand substrate is typical of Habitat Two and gives protection to *Lophopanopeus bellus diegensis* and small *Cycloxanthops novemdentatus*. The current pattern in a channel situation is not readily likened to habitats visited by the writer in tropical waters, though such a complex probably exists along the reef at La Paz, Baja California, Mexico, and in other areas.

GENERIC SPECIFICITY OF HABITAT

Lophopanopeus leucomanus. Of the two subspecies of this species redesignated by Menzies (1948), *L. l. leucomanus* was found in great abundance locally, while specimens of *L. leucomanus heathi* were collected only in Bay Two, Palos Verdes, California. *Lophopanopeus l. leucomanus* was found most abundantly in Habitat Two, where it occupied small spaces under rocks. Often this crab was obtained nestled in piles of drift algae or buried directly in the sand beneath rocks, or under pitted rocks laid over a rock substrate, or in a network of snail tubes. Occasionally adults of this species were collected in what would be classed as unprotected rocky coasts. However, a close examination of the position of boulders in relation to the wave action and of the species of algae present revealed that these crabs were within a micro-habitat typical of a protected coast. Some adults were also found in and about the rocks and tube-snail masses in Habitat One. The very early crab stages of this species were found in tiny crevices under rocks, in tube-snail masses, or in the dense stolons of the *Gigartina* turf of Habitat Two and in the coralline turf of Habitat One.

The writer dredged *Lophopanopeus l. leucomanus* from various depths to a maximum of 55 fathoms in the San Pedro Channel while on board the "Velero IV." Menzies (1948), in his revision of the genus *L. leucomanus*, examined 311 specimens of this species, which at that time was the total number on deposit at the Allan Hancock Foundation. A somewhat erroneous picture of the major habitat of this species is obtained from Menzies' statement that only 26% of the specimens were from the intertidal zone and 74% from deeper water between 10 and 110 fathoms. An examination of the station list used in that publication revealed that 36 of the 62 stations were dredge hauls while only 26 were shore collections. Furthermore, the highest number of specimens from the three most productive dredge stations was 18, 20, and 102, while the three most productive shore stations produced 10, 12, and 18 specimens, the dredge having sampled an area of 4 ft by roughly 0.5 mi per station while a shore station covered considerably less area. In addition, the percentage of total dredge hauls which contain *L. l. leucomanus* was much smaller than the percentage of shore stations with this species.

However, these data demonstrate that *Lophopanopeus l. leucomanus* is not euryzonal, although it can survive and reproduce at great depths when the megalops are forced to settle and metamorphose there. The extremely small size of ovigerous females and

mature males and the absence of any large specimens indicates that the deep water members are inhibited in their growth by atypical benthonic conditions.

Lophopanopeus bellus diegensis. This species was observed at Habitat Three at Corona Del Mar, California. Here the crab was most abundant below the +6 in tide level. Larger specimens were found burrowed into the sandy substrate beneath rocks. Medium and small-size specimens were most common in the snail-tube masses which fringed the bottom rocks. Some were also found in the tube masses of the channel sides. Apparently all of the life activities of adult specimens are carried out in the protection of such rock masses since the flat sand bottom offers no protection from current or predators.

The writer has dredged numerous specimens of this species in water to a depth of 10 fathoms from a substrate of pitted rock and sand. In the shallower hauls fronds of red algae (not identified) were present and may have served as food. In all cases mature females were smaller than the average ovigerous females of the intertidal zone. Menzies (1948) examined 517 individuals of this species; he lists 86% as collected below the intertidal zone (down to 100 fathoms) and 14% from shore collecting. However, a check of his station list reveals that of the 64 stations 7% are without depth data, 12% were shore stations, and 81% were deep water. When station percentages are correlated with specimen percentages, the evidence that this species lives primarily in deep water vanishes. This species is able to survive at deeper levels, however, and appears to be less abundant along the intertidal zones of bays, harbors, and channels than *Lophopanopeus l. leucomanus* is along the open coast. The writer believes that *L. bellus diegensis* was originally more common in the intertidal habitat. Industry and increased human populations, perhaps, have changed or eliminated the habitat of this species in California by pollution or harbor alteration. Thus in numbers this crab is important, but to a lesser degree than those xanthid species of the open coast.

Paraxanthias taylora. Optimum ecological conditions for this crab are found in Habitat One among the large algal covered boulders. Unlike *Cycloxanthops novemdentatus* which dwells between the deepest boulders and the coarse sand substrate, *Paraxanthias taylora* occupies a niche high up in the layers of boulders near the algal turf. Typical of all Xanthidae, this species dwells in small pockets which are formed by irregular surfaces of two or more adjoining boulders and afford a maximum of protection. Often a sponge, tube snails, or a small stone wedged between two larger rocks help to form a floor or wall of their grotto. The pocket is usually of such a nature that the crab can fold its chelae to block the entrance and thus ward off enemies. At high water this species can be seen peering out of its hiding place, and occasionally feeding on small algae which grow on the rocks.

In Habitat Three, small *Paraxanthias taylora* are

common, though found exclusively in the snail-tube masses on the side of the channel wall. No specimens have been found between bottom rocks and the sand substrate, where *Lophopanopeus l. leucomanus* and small *Cycloxanthops novemdentatus* are abundant. Again the affinity for a higher niche is significant and may be a response to the microalgae and numerous hiding places found there.

All size classes are abundant in the same general niche, each occupying a small protected pocket suited to its size. Ovigerous females are in great abundance in season and their presence suggests that there is no migration to deeper water for reproduction as in the case of *Cycloxanthops novemdentatus*.

Occasionally *Paraxanthias taylori* can be found under rocks near unprotected headlands. This situation does not appear to be ideal as testified to by population densities in this zone when compared with Habitat One. *P. taylori* has also been recorded from deeper water. The writer has collected specimens in 15 ft of water by pulling up *Macrocystis* holdfasts. Rathbun (1930) records this species as being obtained down to 55 fathoms. As is typical of *Lophopanopeus b. diegensis* these deep water specimens are smaller in size and in general less well developed than intertidal specimens; thus, they are probably not well adapted to a deep water existence.

Cycloxanthops novemdentatus. Juvenile and small mature *C. novemdentatus* are, in general, the only size classes of this species encountered throughout the year in the higher, protected rocky-coastal zone such as Habitat Two. These small, multi-colored crabs are found in coarse shells and sand beneath large rocks, or in small spaces between pitted surface-rock and a solid substrate. The variously mottled colors of the small crabs often blend closely with their immediate surroundings, making them difficult to see. The crabs generally hide with their carapace against the rock cover. When the rock is removed the crab is seen in a small depression of dimensions which slightly exceed those of the crab.

Larger monochromatic *Cycloxanthops novemdentatus* do not dwell above the zero tide level but seek deeper water from a -1 ft tide to a -4 ft level. This zone is typical of Habitat One or the seaward side of Habitat Two. The hiding place of this species is again associated with the substrate and is not up between the layers of boulders. The crabs hide in small natural pockets beneath rocks or in the lowest pockets formed between rocks, or they excavate a small grotto, or bury themselves in the sand beneath a rock. From their hiding places the larger *C. novemdentatus* move along the lower edges of rock formations or move up through a series of passageways in order to feed on small, fleshy, rock-inhabiting algae, but return to their hiding place for periods of inactivity.

On certain occasions larger, monochrome *Cycloxanthops novemdentatus* were collected in goodly numbers occupying under-rock spaces at about the +1-ft-6-in. level, but were absent at other times. Among these were males up to 100 mm wide (the largest

previously on record is described by Rathbun (1930) as "an unusually large specimen of extraordinary width," which measured 94.1 mm). After many months of observing the appearance and disappearance of these large crabs, it was concluded that these specimens had migrated inshore to molt (Knudsen 1957), since all were in the pre-molting, molting, or post-molting condition. Each occupied a rather large sub-rock space, the entrances of which were packed with drift algae. From the large number of crabs found at low tide which had shed their exoskeleton within the previous hour, it was concluded that many of these crabs shed during the absence of heavy surf action, and were then able to harden sufficiently to bury themselves before the return of high tide.

The absence of ovigerous female *Cycloxanthops novemdentatus* from general intertidal collections is striking. From 61 Allan Hancock Foundation shore stations at which a total of 327 (138 ♂♂, 99 ♀♀, and 90 juveniles) were collected, only one gravid female was found. The writer examined many hundred individuals of this species from Habitat Two but found no females with eggs. Ovigerous females were obtained only by skin-diving to the -2.4 ft levels at the Palos Verdes site. However, at La Jolla Caves during a low September tide, gravid females (8 collected) were found in great quantity at a -2 ft level.

Hence the deeper habitat zone, seldom exposed by low tide, is occupied by the large monochrome specimens of *Cycloxanthops novemdentatus*, while small, polychrome individuals inhabit areas typical of Habitat Two. Schmitt (1921) and Rathbun (1930) list this species as (exclusively) intertidal, and the Hancock Foundation has no specimens obtained by means other than shore collecting. Actually, where situations such as the habitat at Bay Two and Bay Four do not occur, these crabs may extend several feet below low low-water. While diving the writer observed one specimen at a depth estimated to be near -6 ft.

HABITS AND BEHAVIOR

LOCOMOTION AND PEREIOPOD ADAPTATIONS

Locomotion of Brachyura restricted to an aquatic existence has been investigated by Bethe (1897) and List (1897), while the locomotion of a land crab, *Ocypoda arenaria*, was studied by Cowles (1908) and that of an intermediate land and aquatic form, *Pachygrapsus crassipes*, was studied by Hatt (1948). The California Xanthidae are typical of most Brachyura in that they use the last four pairs of pereopods for ambulation while they use the first pair (the chelipeds) in a variety of functions: defense, feeding, excavation, balancing, and mating. Normally xanthid crabs run or walk sideways, but they frequently move backward, or occasionally walk forward.

For random wandering or swift movement such as fleeing or pursuing, the crab moves in a lateral direction. This mode of movement allows the crab to attain greater speed, or to direct its smallest dimen-

sions forward, thus permitting it to pass through smaller spaces. The first three pairs of ambulatory legs are used extensively in walking, while the last pair is directed posteriorly and is moved irregularly above the substrate. The first and third pairs of legs are used independently, rotating from pair one, to pair two, and to pair three in rapid order. The chelae generally are held close to the cephalothorax so that the weight is distributed over the second pair of walking legs. If the chelae are extended, as in a defensive action, the first pair of ambulatory legs is placed ahead of the body so that balance is maintained while moving. At such a time the fourth pair of walking legs is often placed on the substratum and used in ambulation.

The chief function of the fourth pair of legs is unique and is well adapted to life in the xanthid habitat. This pair of legs is held above the substratum, and is directed posteriorly, being moved irregularly while the crab is in motion. It serves in a sensory capacity, feeling posteriorly until some solid object, such as the side of a rock, is contacted. At this time the fourth pair of legs "walks" along the solid wall behind the crab and tends to make it aware of changing contours. Blinded crabs move in an identical manner and follow the irregular shapes of rocks with no apparent difficulty or loss of speed. In combat, or while feeding near rocks, the last pair of legs is used in an "ice-tong" fashion to hold firmly to rocks or other suitable objects.

Perhaps the most peculiar function of the fourth pair of ambulatory legs is seen when the crab is within a small tunnel or space between two rocks. At such a time this pair of legs is held high over the back with the propodi and dactyli directed upward. Thus, in walking through a narrow passageway, the fourth pair of legs literally walk on the ceiling while the first three pairs of ambulatory legs walk on the floor. As waves pass the habitat the four pairs of legs are extended, thus lodging the crab firmly and protecting it from surf action.

Aside from the common lateral movement, xanthids move freely forward or backward on such occasions as in stalking food, mating, or in defensive action. In a forward movement the body weight is carried on the second and third pairs of legs while the first pair is moved forward. The second pair is then moved forward and the weight is maintained on leg pairs one and two until pair three is moved up to the starting position. This process is then repeated as the crab moves forward. Backward movements are just the reverse of this process; the third pair of legs leads off while the fourth pair is held high and is directed posteriorly. While so walking the chelipeds are alternately placed against the substrate and used to push the crab backwards. During times of danger the xanthid crabs may assume a defiant pose with the horizontal plane of the cephalothorax held vertically and the chelae raised up and forward of the oral area. At such times the second and third pairs of legs carry the main body weight

while the first and fourth pairs touch the substrate to balance the crab.

Xanthid crabs do not swim as a normal means of locomotion, nor are their appendages adapted for it. Crabs which are exposed when the rock under which they are concealed is removed sink slowly to the substrate and make no attempt to swim. The chelae are used to balance the crab as it sinks, by flexion or extension. In an experiment all of the species of xanthid crabs were released in a heavy surge which provided a strong current. In each case the chelipeds were used to stabilize the crab and to keep it upright until it reached the substrate. If swept along the substrate the chelae function as a "sea anchor." However, at no time did any xanthid crabs attempt to cling to algae with their chelae as they were swept past. Instead they made an attempt to get under a rock or bury themselves in the sand if a rock was not near.

All of the local xanthid crab species will quickly bury themselves when a suitable hiding place cannot be found. In nature this ability is most important to *Cycloxanthops novemdentatus*, which lives in association with a sand substrate, next important to *Lophopanopeus*, least important to *Paraxanthias*, which dwells above the sand substrate in rock piles. The procedure of burying itself in the sand is the same for all xanthid species. The crab settles close to the sand with all pereopods against the body. The legs are then extended, pushing the sand away from the body. The sand is then held away by the meral and carpal segments of all legs while the propodi and dactyli are again folded under the body to scoop out a new load of sand. As the process is repeated the manus of the chelipeds is flexed and extended in such a manner as to push sand from under the body, and to force the body posteriorly into the sand. These functions are carried out rapidly, enabling the crab to bury itself in a matter of seconds. *C. novemdentatus* is well adapted for this practice in that the legs have margins of stiff "hairs," which serve to increase the width of the legs and thus aid in lifting sand from beneath the body.

FREEZE RESPONSE AND AUFBAUMREFLEX

Closely related to locomotion, or the lack of it, is the curious "freeze response" of the Xanthidae. It is common for a collector to overturn a rock in the lower intertidal zone and observe a substrate of gravel, a piece of which seems suddenly to acquire legs and metamorphose to a small xanthid crab. This is especially characteristic of *Cycloxanthops novemdentatus* and *Lophopanopeus* spp., less so of *Paraxanthias taylora*. Multicolored members of the first two genera appear to "freeze" and remain motionless when the rock under which they are hiding is removed. This, however, is not fully the case, but rather the degree to which the freeze response is initiated is proportional to the state of concealment prior to the disturbance. Crabs fully buried (completely enclosed by sand or drift algae while beneath a rock) are very

reluctant to move at all. Crabs occupying a small subspace (without sand or algae enclosing it) remain motionless for a brief time. Crabs taken by surprise while actively feeding make no attempt to freeze, but run swiftly to seek new concealment.

The freeze response, as so described, is never encountered under water during high tide. Without exception xanthid crabs which are uncovered make an attempt to run and hide. This suggests that the crabs either use this type of response only at low tide, or that all crabs observed were in an active state. Experiments to test these suggestions, however, were not completed. It is remarkable to note that the frequency with which this response is encountered decreases greatly during the spring and early summer, for at these times there is a marked temperature increase and an increase of crab activity as well, suggesting a correlation between inactivity and the response.

The freeze response could logically be triggered by several things when the crab is suddenly exposed: increase in light, movement perceived visually, or mechanical disturbance. The following experiments were devised to test more specifically the nature of the stimulus involved.

Experiment A-1. Xanthid crabs were placed in finger bowls supplied with sea water and placed in a large box. A lid was hinged to the top of the box and a few small peep-holes cut into the box for light and observation. When the crabs were settled the lid was removed, at which time the crabs froze for several seconds.

Experiment A-2. Xanthid crabs were placed in a large, full aquarium which contained no sand or rock. The room was then almost totally darkened. (Enough light was required for the observer to see the crabs.) When the crabs were active a bright light was turned on at which time all crabs froze to some degree. The larger crabs remained motionless longer. This experiment was repeated several times after a few minutes' interval, and the response to the light was successively less pronounced.

Experiment A-3. The same equipment was used as in experiment A-2, but rocks were added, and after several minutes the light was switched on. Crabs partly concealed moved somewhat to better hide themselves (pulled in their chelae or legs, or backed under a rock). Crabs that were well concealed or completely exposed became motionless. Exposed specimens soon moved away from the light. This movement of partially concealed crabs was frequently observed in nature.

Experiment A-4. Crabs were placed in a medium-sized aquarium in a lighted room. A stone suspended by a string was placed in the tank. The other end of the string passed through a pulley and to a blind where the observer was concealed. When crabs were actively moving about in the tank the small stone was raised, its movement causing a momentary freeze response of the crabs near by.

Experiment A-5. This experiment utilized the

equipment of A-4, but did not have the stone in place. When the crabs were active, the observer stepped from concealment and approached the tank. At such times the crabs became motionless, buried themselves, or moved closer to a rock hiding place. In the field similar responses were encountered when the observer swam or waded close to an exposed or partially concealed xanthid crab. The crab usually stopped all activity for several seconds, and then darted into hiding. If the observer swam directly to the crab in an effort to catch it, the crab generally did not "freeze" but ran for concealment.

Experiment A-6. Xanthid crabs were placed in a large aquarium equipped with some stones for hiding places. Into this tank was placed a large *Cancer antennarius* which attempted to catch the xanthid crabs. Smaller xanthid crabs ran for concealment as the *Cancer* approached. Larger crabs, which had no hiding places, pressed into corners to hide, or remained motionless while the *Cancer* passed them by. They then "drifted" off by using such small steps, keeping their legs so close to the body that leg movement was barely noticeable.

Experiment A-7. An aquarium was set up like that of experiment A-6, but a large *Pachygrapsus crassipes* was used in the place of *Cancer antennarius*. The grapsoid moved to the corner of the aquarium and remained motionless behind a large rock. In a short while, a medium sized *Lophopanopeus l. leucomanus* moved around the rock which hid the grapsoid crab. When *Pachygrapsus crassipes* was in view the xanthid crab froze with both chelae outstretched, and remained that way for seven minutes. In the meantime, a small *L. l. leucomanus* moved around the rock in front of the grapsoid crab, and was caught and eaten. Later a *Pararanthias taylori* approached *Pachygrapsus crassipes* but did not freeze.

Experiment A-8. At various times during activity and inactivity the xanthid crabs were mechanically prodded. The nature of response varied from a complete freeze response to an attempt to escape.

These observations are not conclusive, but they suggest that changes in light intensity, visible movement, or mechanical disturbance work singly or in combination to produce the freeze response. Experiments A-1, A-2, and A-3 show that a change in light intensity is enough to cause a freeze response identical to that observed in nature. Experiments A-4, A-5, and A-6 show that movement of various objects which do not mechanically disturb the crab will also trigger this response. In experiment A-7 the sight of an enemy was enough to cause one crab to be motionless for seven minutes while others were not affected by this. Finally, experiment A-8 shows that prodding plus the sight of a moving object will cause a natural freeze response.

The freeze response is probably not an attempt to feign death, as is the case in *Hemigrapsus nudus* (Hiatt 1948), but rather an attempt to remain concealed. It is interesting to note that the age-class and species of crabs (young *Cycloxanthops novem-*

dentatus and *Lophopanopeus* spp.) which rely the most upon this behavior are multicolored individuals so mottled as to resemble the pebbles among which they hide. During this response the crabs in question appear alert: their eyes follow movement and their antennules and antennae frequently move. If, after several seconds of inactivity, they move to seek better concealment, they do so in a secretive manner. If the process of escape is interrupted, the crabs react in several ways: they run, they "freeze," or they assume a defensive attitude designated by Bethe (1897) as the "Aufbaumreflex." The crab elevates itself upon its dactyli, extends its chelae upward and outward, and elevates the body proper. If further molested, a large *C. novemdentatus* will attempt to pinch as it runs away. During high tide, this species will quickly manifest the Aufbaumreflex even though untouched by the observer. Thus, under water large *C. novemdentatus* react differently, in a manner more typical of grapsoid crabs.

CATALEPSY-LIKE RESPONSES

A third and different reaction was noted many times when working with *Cyclozanthops novemdentatus* in the laboratory and on occasion in the field. If injured or roughly handled the animal frequently manifests what might be called a "catalepsy-like response." The legs are flexed or extended in a state of tetanic contraction and the animal seems to lose all awareness of its surroundings. The pereopods become so rigid that the crab can be held up at any angle by the tip of any single walking leg, or by the claws of its chelae. The crab can be placed upon its "face," upside down, or in any other position either in or out of the aquarium, where it will maintain this response for some time. Furthermore, the animal does not react to movement before its eyes, or to light change, but rather seems totally unaware of these. If the crab is left in this condition for many minutes, or if the legs are tapped, it will regain its awareness and return to normal. It was noted that the animal will re-enter this state of stupor and contraction a second and third time with but a fraction of the stimulus required for the first response.

The exact initiating stimulus which triggers the catalepsy-like response is not known. After much antagonism or maltreatment the animal appears overcome by a state of violent alarm. The speed with which the threshold is reached depends upon the nature of the treatment. In the instances mentioned above, the threshold was reached in a matter of minutes or seconds. However, when the water in the aquarium is allowed to evaporate until the salts reach a near-lethal concentration (76.2 ‰) over a period of 3-4 wks, the xanthid inhabitants become stupified and enter into a state of tetanic contraction. No logical demonstration of any life-preserving mechanism has been made by the observer. It would seem more fitting to say that this response, unlike the prior two, has its origin in a set of purely physiological condi-

tions rather than in a reflex protective mechanism; but tests to substantiate this have not been made.

VISUAL, CHEMICAL, AND TACTILE SENSES

The xanthid eye. The eyes of the California Xanthidae consist of clusters of ommatidia grouped at the distal end of a pair of eyestalks. The visual acuity of a compound eye is indirectly proportional to the angle between two ommatidia. Hence the faceted surface of the eye with the least amount of curvature directs more ommatidia to a unit of space, and is capable of greater photoreception from that area. Fig. 8 shows the comparative amount of curvature and distribution of the faceted surface of the eye of *Cyclozanthops novemdentatus* which will also represent the other genera. The eye is situated in a socket produced by the carapace. There it can be directed vertically or horizontally, or drawn laterally into the socket for rest or protection. An inspection of Figure 8 (A through E) shows the lateral and anterior surfaces of the eye to be flattest and best supplied with ommatidia, though ommatidia are also directed dorsally, ventrally, and posteriorly. As previously noted, locomotion is generally lateral, or in the direction of the greatest concentration of ommatidia. Likewise the flattened anterior surface is well suited to observe approaching enemies, and possible food sources. This distribution of ommatidia is typical of *Pachygrapsus crassipes* (Hiatt 1948) but differs from that of *Ocypoda arenaria* (Cowles 1908) somewhat in that more ommatidia are directed dorsally and ventrally.

Smaller xanthid crabs are probably more dependent on visual perception than larger and stronger specimens. They have more enemies and competitors and are seen to be more active than older crabs. Thus they have more need of a warning mechanism such as vision. Larval and young crab stages have more faceted surface per unit of body size than older specimens. Table 1 shows data obtained from measurements of small *Paraxanthias taylori*, where the carapace length and width, the eyestalk length, and the distance between the tips of the eyes are given. Since the faceted area is generally proportional to the length of the eyestalk, it is convenient to use the eyestalk length as an index of the faceted area, and to express this as a per cent of the carapace width. An inspection of the right-hand column of this table shows the great reduction of ommatidial surface with the increase in carapace width.

Perception of movement. The xanthid crabs are very quick to detect any movement of either object or shadow. The writer has had occasion to spend many hours observing *Pachygrapsus crassipes*, *Grapsus grapsus*, *Ocypoda occidentalis*, and other grapsoid crabs and was greatly impressed by their alertness and swift reaction. The Xanthidae are probably equally alert, but this is not always observable because of the variety of responses given. Frequently these crabs react with the freeze response and do not move at all, while at other times they run away and

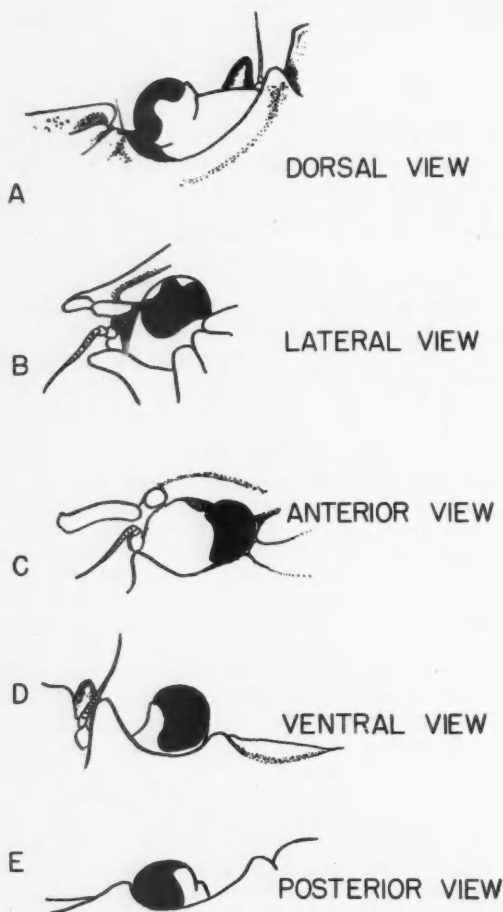


FIG. 8. Aspects of the eye of *Cycloxanthops novemdentatus*.

TABLE 1. Change in faceted surface with increase of body size in the xanthid crab *Paraxanthias taylora*. Eystalk length as a % of carapace width is used as an index to the total faceted surface.

Crab Stage	Carapace Length (mm)	Carapace Width (mm)	Eystalk Length (mm)	Distance Between Eye Tips (mm)	Eystalk length as % of Carapace Width
Megalops.....	6.0	3.9	1.70	5.4	43.5
First Crab.....	5.2	6.0	1.50	6.0	25.0
" "	6.0	8.5	1.60	6.7	18.8
" "	7.0	10.0	1.65	7.7	16.0
" "	8.0	12.0	1.75	8.7	14.5
" "	8.7	13.0	1.85	9.2	14.2
" "	9.4	14.0	1.96	9.8	13.9

hide. Experiments listed for the freeze response show the alertness with which movement is detected by the Xanthidae. The writer has observed this on many occasions while swimming in deep water over the xanthid habitat. Active crabs stopped all movement and dashed for cover when the observer moved his

hand. New activity was halted again and again by a mere hand movement. In the laboratory all activity can be stopped by switching on a light or by causing a shadow to fall near the crab.

Locomotion and concealment. The eyes are not of great importance in locomotion except, perhaps, to determine the ultimate destination. Crabs that are blinded by coating their eyes with aquarium cement are able to run and walk with no apparent difficulty or loss of speed. The fourth pair of walking legs is used to direct the crab around contours or through small crevices. One *Cycloxanthops novemdentatus*, with its eyes removed, lived in the aquarium for three weeks and another for seven weeks. Both fed and defended themselves in a normal manner.

An observer of the California species of Xanthidae could not fail to notice the swift manner in which they can find a new place of concealment. On one occasion the writer transported a dozen crabs of each genus to a new habitat area and released them one at a time. In each case the individual ran to a place of hiding with little or no hesitation. The following tests were conducted to determine if the crabs see a hiding place as such, or if they are directed by corresponding light intensities, since the hiding place, being a cave or crevice, is dark and appears as a black area.

Experiment B-1. Several "caves" were constructed of dark rock in a large aquarium into which xanthid crabs were released. In most cases they ran directly to the caves and entered them. Some crabs, however, ran to darkened corners of the aquarium.

Experiment B-2. Caves made of white clay were placed around the entire periphery of a very large, round aquarium, and light was allowed to enter the back of the caves through the aquarium wall. When different xanthid crabs were released they wandered more-or-less aimlessly to the side of the aquarium, turned so they faced the center, and with the fourth pair of walking legs located and entered the caves.

Experiment B-3. The same equipment from the last experiment was used, but the entrances to some caves were blocked with dark stones. In all cases crabs of the different genera ran to the dark stones, then turned when they could not enter and felt them with the last walking legs. Some crabs remained by the dark stones, others located open caves by tactile examination.

Experiment B-4. Xanthids that were placed in a clean tank wandered aimlessly or did not move at all.

Experiment B-5. The wall of a large circular tank was lined with alternate strips of black and white paper. The different xanthids were released in the center of the tank one at a time to test their reaction. With only one exception all ran to the black strips and remained there.

These experiments, together with field observations, indicate that the Xanthidae are guided to hiding places because they are dark and appear as black areas rather than actual crevices. The tactile sense

is used secondarily to "feel" for places in which to hide.

Vision. Some underwater observations in the field suggest that *Cycloxanthops novemdentatus* may "recognize" animals as possible food sources. Large members of this species were seen on many occasions to pry at small abalone (*Haliotis cracherodii*) which adhered to rocks. The crabs made no great show of this but tried to dislodge them as they walked along. Though these xanthid crabs were never seen to free an abalone, several abalone were found which had unmistakable chela marks in the partially eaten foot which may have been made by xanthid crabs. *Cycloxanthops novemdentatus* have also been seen breaking open live sea urchins (*Strongylocentrotus purpuratus*) upon which they fed. Apparently the crabs recognized the abalone and urchin through some visual pattern or image or through chemical stimulation.

Compensatory movements. All members of the California Xanthidae display the compensatory movements of the eyestalks noted for other Decapoda (Bethe 1897, Clark 1896, Cowles 1908, Hiatt 1948, Lyon 1899). Fig. 9 shows, diagrammatically, the more common movements observed. (The length of the eyestalks is much exaggerated.) Fig. 9A illustrates the normal eyestalk position at 45° from the horizontal body plane. In this position the maximum area of faceted surface is directed in all of the required planes of vision (Fig. 8).

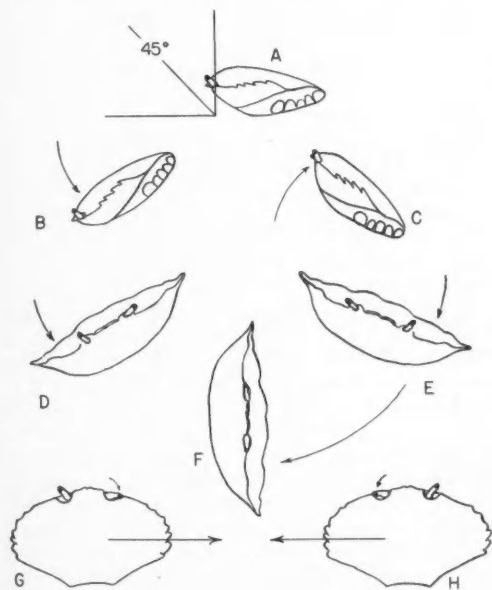


FIG. 9. Compensatory movements of the eyes. See the text for an explanation of this figure.

When the anterior part of the carapace is tilted down (Fig. 9B), the eyestalks are raised to almost 90° above the longitudinal axis of the body. Like-

wise, if the body is tilted backward and upward (Fig. 9C) the eyestalks come to rest just slightly above the longitudinal axis. When the crabs move about in such a way that the body is tilted, the eyes quickly compensate as described. As a *Paraxanthias taylora*, for example, moves up an incline between two rocks, the eyes are moved forward, thus allowing the crab to observe a maximum amount of its surroundings without exposing much of its body. After a brief inspection the eyes are rotated a few times before the crab finally ventures out to feed.

When a xanthid crab is tilted to the right or left (Fig. 9D,E) the eye on the upward side is lowered while the eye on the lower side is raised. However, if the body is tilted further (Fig. 9F) both eyes are drawn into the groove provided for them in the carapace.

When a xanthid crab moves rapidly sideways, (Fig. 9G,H) especially if entering a hiding place, the leading eye is lowered while the trailing eye is elevated. Though the xanthid eyestalks are very short and well protected at any angle, this type of compensation may prevent damage to the eye, as is the case in *Ocypoda* (Cowles 1908).

Orientation. In an experiment designed to give some information on hiding activities, 24 xanthid crabs were placed in an aquarium which contained a few algae-covered rocks. The laboratory was darkened except for one light beneath the aquarium. After an hour it was noted that 18 of the crabs hid beneath the rock in spite of the reverse in light direction. Two *Cycloxanthops novemdentatus*, however, turned upside down so that the light struck their eyes from the normal dorsal direction. This suggests that light may be a factor of orientation for the Xanthidae. The following experiments were devised to test this suggestion further.

Experiment C-1. Crabs were "blinded" (eyes covered with aquarium cement) and placed in aquaria with sand substrata. These individuals were turned over repeatedly, but they righted themselves very quickly. They walked and moved normally. Individuals from which eyes were excised were tested. These also righted themselves instantly upon being turned over. Furthermore, after three days, and again after two weeks, their reactions were equally quick and accurate.

Experiment C-2. Crabs which were "blinded," and with their statocysts removed, were placed in aquaria like those used in Experiment C-1. Upon being turned over these crabs righted themselves, but they faltered as if the technique for righting was new and had to be tested each time. Occasionally they were not able to right themselves at all, and remained upside down. Walking and running were normal, but they lost their balance and fell over with every sharp turn or change in bottom contour.

Experiment C-3. The same crabs and equipment of the last experiment were used except that the crab's "blindners" were removed. When turned over these crabs were somewhat less awkward in righting

themselves. Running was accurate but again the crabs were not surefooted and lost their balance frequently.

Experiment C-4. A clean aquarium was furnished with a large, oval rock. The rock, being convex on the bottom, rested on its center but left a considerable gap between it and the tank at its periphery. Blinded crabs with the statocysts removed were placed upside down on the clean glass of the aquarium just under the edge of the rock so that their walking legs touched the underside of the rock. Crabs in this condition walked around the periphery of the rock for over half an hour. As they walked, their dorsal side slid along the floor of the aquarium. Not once did they right themselves until, after one half hour, the rock was removed. When these crabs were turned upside down again they floundered somewhat, but righted themselves.

Experiment C-5. The same crabs and equipment as in experiment C-4 were used except that the blinders were removed. When turned over the crabs righted themselves. However, when turned over and placed so that their feet contacted the underside of the rock they remained there up to fourteen minutes before righting themselves.

Experiment C-6. Normal crabs were turned upside down and placed under the rock used in the last experiments. They remained this way only until there was no movement in the tank or laboratory. When all seemed "safe" they quickly righted themselves and backed under the rock again.

Experiment C-7. Blinded crabs which had normal statocysts present were turned over and placed under the edge of the rock. These crabs quickly turned right-side-up. When turned on their "back" again they quickly righted themselves.

Originally it was seen that a few xanthid crabs oriented themselves upside down so that the sub-light became dorsal to their eyes. However, when the eyes (C-1) were removed, and when the eyes and statocysts (C-2) were removed the crabs still maintained the proper orientation. Likewise, the removal of statocysts alone had no effect on normal orientation, thus suggesting that a tactile sensation may play a dominant role in orientation. Further insight was gained when a rock overhang, against which the crabs could flex their legs, was substituted for the normal substrate. When the eyes and statocysts were removed (C-4) the crabs remained upside down indefinitely until the rock against which they were pressing was removed. However, normal crabs, or crabs with only eyes or statocysts removed, did not remain upside down but righted themselves. This suggests that the sensation of the legs against a solid substrate is a requisite to orientation. When this condition is fulfilled, the visual or balance centers take over in determination of orientation, and are thus probably secondary in this matter.

The statocysts are very important in balancing as the crab maneuvers about its habitat. When the statocysts were excised, the crabs could not run and turn

sharply without falling over. They fell off of slight declines, fell over backwards when stopping quickly, and so on. The present writer removed the statocysts from *Pachygrapsus crassipes*, a very agile and swift crab which spends much time darting around rocks. The results were the same, for while the crab was very swift it could not turn well, and fell over or ran against the rock about which it was darting.

Tactile senses. The tactile senses of the California Xanthidae are very well developed and play a major role in normal adjustment to the environment. The Xanthidae are generally well provided with sensory "hairs" and bristles on the appendages and body parts. By these they are made aware of solid objects which they contact, objects which contact them, water movement, and many other things. As noted, blinded crabs with the statocysts present can maneuver very well, feed, and carry on an otherwise normal life. When the eyes are excised the individual becomes extremely sensitive and even pugnacious (a response not normal except at certain times). The blinded crab turns swiftly, raises its chelae and stands ready for defense the instant it is touched on any part of an appendage, especially the dactylus. If touched by a piece of seaweed the crab will grasp it and will not release its hold until it is apparent that there is no resistance. When touched by other crabs the blinded crab "locks-on" to the assailant and will hold it for several minutes. However, when the normal crab remains passive (as is usually the case) the blinded crab releases it.

During one 3-hr underwater observation of a xanthid habitat it was noted that most of the movements made by *Paraxanthias taylori*, and to a lesser degree by *Cycloxanthops novemdentatus*, were made between wave periods. For example, as a *P. taylori* moved up through a column of rock to feed it walked several steps but stopped as the wave-crest passed over the area. When the wave was past, the crab took several more steps until the next wave came. This was not true of all observations but at times the synchronization with wave action was quite noticeable.

Such activity suggests that water current, either kinesthetically or by movement of the tactile hairs, stimulates the crab and causes it to extend its legs, thus securing its position. An attempt was made to reenact this in the laboratory, but the results were not consistent. Crabs were placed in small "caves" constructed from rock. A jet of water (gravity flow) was directed against the legs of the crabs in a periodic, wave-like fashion. On occasion leg extension coincided directly with water release, but frequently the results were negative. When a stronger, freshwater jet was used the reaction was somewhat stronger but not definite. It was apparent that wavelike force could not be duplicated without running salt-water and other marine-laboratory equipment, thus further experiments were not attempted.

Leg "hairs" are well developed in most of the xanthid crabs found about Los Angeles, but are

sparse, or absent in some species of *Lophopanopeus*. Body "hair" may be sparse except in *Pilumnus spinohirsutus*, but is present in all xanthid crabs on the sub-branchial region about the coxae of the pereopods. There are also 8-10 small tufts of sensory "hairs" on the dorsal surface of *Paraxanthias taylora*. These are located between the cardiac and urogastric areas, between the mesogastric and protogastric areas, and between the posterior protogastric and epibranchial areas of the carapace. These tufts of "hair" are extremely sensitive to touch and to water movement, and may well serve as "wave receptors."

Food procurement. The close integration of the visual, chemical (taste and smell) and tactile senses is clearly seen in the investigation of activity which aids the xanthid crab in search of food. The California Xanthidae possess and use all of the senses ascribed to other crabs in obtaining food. As will be discussed later, these animals are chiefly herbivores which reside within a few inches of lush algal growths. However, part of their diet consists of animal tissue caught alive, or found as detritus which is washed into their habitat. Thus the question arises as to which sense governs the discovery of their food.

Many cases of cannibalism and depredation have been witnessed in the laboratory. Smaller crabs which pass too close to the hiding place of larger xanthid crabs are, at times, caught, crushed, and fed upon. It would then seem that the location of such food is done primarily by the sense of sight.

Herbivorous activities are probably carried out with the aid of all three senses. Blinded crabs were seen to feed normally. Twelve xanthid crabs kept in total darkness for 10 days ate the daily ration of marine algae given them, even when it was put in places judged difficult to find. Likewise, crabs gleaned algae from rocks while in total darkness. It is difficult to say whether the chemical or the tactile sense was of primary importance. It is not known (1) if living alga has any "odor" which may diffuse to the crab and thus guide the crab to it, or (2) if the plant is found tactually, tasted, and finally eaten. The idea that the consistency of the fleshy algae is used as a criterion by the crab is not altogether sound for the xanthid crabs eat a good deal of articulate coralline algae which has the consistency of sand grains.

Several experiments were conducted to gain some idea of how the location of non-vegetable matter might take place. These experiments were worked in the field with *Paraxanthias taylora* and *Cycloxanthops novemdentatus*, and in the laboratory with all three major genera. The field experiments were conducted in Bay Two over the large xanthid habitat when there was about 5 ft of water above the substrate. Food materials were kept in waterproof containers (attached to the innertube raft) in order to keep a surplus of meat juice from the experiment area.

Experiment D-1. A piece of fresh abalone (*Haliotis cracherodii*) was allowed to sink between some rocks in "Bay Two." In about one minute small

shrimp (*Spirontocaris* spp.) appeared and began feeding. Shortly after this several blennioid fish appeared to compete with the shrimp. About two minutes later a large *Cycloxanthops novemdentatus* was seen approaching the bait from a hiding place which was not in direct view of the baited area. As the crab moved in, the small fish darted away. This experiment was repeated more than twelve times on different days, but the shrimp, fish, crab sequence was generally the same. On one occasion a large Cancer crab dominated the bait. Another time a *Cycloxanthops novemdentatus* chased a shrimp, snapped at it with its chelae, and then took the bait from it.

Experiment D-2. Pieces of abalone viscera were carefully wrapped in cheesecloth and dropped into the xanthid habitat. On different occasions shrimp and fish were attracted, but generally *Paraxanthias taylora* or *Cycloxanthops novemdentatus* retrieved the bait.

Experiment D-3. On many occasions small stones were wrapped in cheesecloth and dropped into the tidepools. The xanthid crabs which investigated these parcels were those which were hiding in view of the "baited area." Parcels dropped into "blind" areas received little or no attention.

Experiment D-4. Light colored stones were smeared with abalone visceral contents and dropped into the habitat areas. Several of these stones were investigated by the xanthid crabs present. Often, upon finding such a baited stone, the crab held it against its mouth parts and cleaned it.

Experiment D-5. Artgum eraser was coated with abalone visceral contents and offered to blinded crabs in the laboratory. On some occasions these were rejected completely, while on others they were cleaned by the mouth parts. No attention was given to uncoated artgum. Blinded crabs either ate or rejected fresh abalone meat.

Experiment D-6. Meat juice was carefully placed on the legs of blinded and normal xanthids. The mouth parts were observed as this was done, but no undue reaction was seen. This was repeated with a carnivorous crab, *Cancer antennarius*. When juice was pipetted to the legs on the right side the crab began a peculiar stamping "dance" with the right walking legs. The mouth parts were also moved vigorously. No such reaction was seen with the Xanthidae.

Experiment D-7. The same technique was used as in the last experiment, but the meat juice was placed so that it reached the mouth parts of the xanthid crabs. At such times the mouth parts moved vigorously and the crab began a restless stamping movement with its pereopods.

Experiment D-8. A series of observations made during normal feeding times, and during other experiments, should be recorded here. Upon dropping a piece of meat of the snail *Jaton festivus* into different tanks, the following observations were made: A *Lophopanopeus* sp. approached and passed by the

meat, then backed up, touched it with its last pair of walking legs, passed it to its mouth, and began eating. *Paraxanthias taylori* and, in other tanks, *Lophopanopeus l. leucomanus* approached a bait from the side, touched it with their dactyli, passed it to the mouth parts, and began feeding. On another occasion a *L. l. leucomanus* cleaned 8 pebbles where a piece of bait had previously been. On the last occasion a piece of bait was put before a large *Lophopanopeus* sp. This crab paid no attention to it until two smaller crabs came out of hiding and tried to drag it off. When this happened the large *Lophopanopeus* chased the smaller crabs away. The smaller crabs were chased away twice more by the large *Lophopanopeus*, which finally ate the meat.

While the foregoing experiments are not fully conclusive they do give a fairly good idea of xanthid behavior under different conditions. Nagel (1894) and Bethé (1895, 1897) agree that *Carcinus maenas* is aided in the search for food by the chemical senses (taste and smell), while Bethé goes so far as to say the chemical senses are the principal ones, the eyes being used little, if at all. This may be very true, if the crab's diet consists of meat fragments only. However, when *Carcinus maenas* pursues smaller Crustacea or other animals as food, which it often does, it is more than likely that the eyes play a primary role. It seems apparent that all three senses are equally important to the Xanthidae and function as an integrated unit or individually depending on the type of food sought and the circumstances under which the searching is carried out. Vision probably dominates in predation and perhaps in daytime foraging. Foraging at night is essentially guided by the tactile and/or chemical senses which aid in the location of meat fragments, as seen in experiments D-1 through D-4. It would appear (D-6, D-7) that the chemoreceptors are well established about the oral region but poorly so on the walking legs, as compared with those of *Cancer antennarius*. The observations presented in experiment D-8 however, suggest that functional chemoreceptors may be present on the walking legs. The fact that untreated artgum eraser was conveyed to the mouth parts further suggests that touch, or the "feel" of food, may be a criterion used in finding food.

FOOD AND FEEDING HABITS

The California Xanthidae are essentially herbivorous, normally grazing on algae growing near their niche or on fronds which have drifted into their hiding place. Secondly, they are scavengers, and thirdly predators, feeding on smaller animals which they are able either to catch or to dislodge.

The method most commonly used for food procurement is the cutting of small segments of algae with the chelae. The stationary "finger" of the chela terminates in a cupped protuberance. The movable "finger" is slightly shorter than the stationary one and thus closes into the cup-like depression, like the

blade of a shears. Hence, the "finger tips" serve to cut the algae and to convey it to the mouth.

Stomach analyses were made on 42 xanthid crabs which were collected early in the morning. The stomachs were removed immediately and preserved in formalin for examination. An estimated 90% of the total stomach content consisted of vegetable matter; two crabs had fragments of small Crustacea in their stomachs. From the contents the following species of plants were identified: *Gelidium pulchellum* (Stackh.), *Gelidium* sp., *Acrosorium uncinatum* (J. Agardh), *Lorenzia* (?) sp., *Pterocladia* sp., *Cladophora microcladioides* Collins, *Corallina vancouverensis* Yendo, *Corallina chelensis* Decaisne, *Corallina gracilis* Lamouroux, and *Phyllospadix scouleri* Hooker. Of the animal tissue recovered from stomach analyses, crab, polychaete, and isopod fragments were found. There was often some sand or mud present. Pearse (1931) estimated the food recovered from another xanthid crab, *Leptodius exarctus*, as 8.5% animal tissue, 66.5% algae, and 25.0% mud and sand. The present writer estimates that 90% of the total food utilized consists of algae and 10% of animal tissue. However, this is based on observations in the field and is not substantiated by the actual stomach analyses.

The most interesting and peculiar thing observed in the feeding habits of the local Xanthidae is the use of coralline algae. Crabs recovered shortly after ecdysis were found to be feeding on almost pure coralline algae. This may be a very rich source of the salts needed to harden and fortify the exoskeleton. Many *Lophopanopeus l. leucomanus* examined were feeding exclusively on crusting coralline algae, while *Cyclozanthops novemdentatus* fed more commonly on erect, segmented forms. Of the total amount of algae recovered from stomach-content analyses about 35% was coralline.

Feeding probably occurs at all hours of the day and night. A great number of xanthid individuals was seen feeding during daylight hours while the writer was swimming under water. However, *Lophopanopeus* was never seen feeding in the field. In the laboratory all of the xanthid crabs were observed feeding during the day and night-time hours. Animals which were recently collected did little daytime feeding but came out of hiding after dark and were then extremely active. Nocturnal feeding seems to be common for the Brachyura in general, many land dwelling grapsoid crabs (Cowles 1908, Andrews 1909, Pearse 1912, Cott 1929, Hara 1933, Hiatt 1948), several spider crabs (Milligan 1915), *Pugettia producta* and *Loxorhynchus crispatus* (observed by the present writer), a canceroid crab *Cancer antennarius* (observed by the writer), and probably many others are more active at night. An attempt to swim in the surf at night to observe the xanthid habitat was abandoned due to safety factors. However, the Xanthidae probably react in nature as in the laboratory aquaria and thus appear to be chiefly nocturnal feeders.

Nineteen cases of cannibalism were seen in the laboratory among *Paraxanthias taylora* and *Lophopanopeus l. leucomanus*. Even more common than cannibalism is the practice of autophagy in which larger crabs molest smaller individuals, forcing them to cast a limb. When an appendage is finally severed at the breaking plane it is eaten by the larger individual.

In the laboratory *Paraxanthias taylora* frequently ate nudibranch eggs which had been deposited on the walls of the aquaria. *Cycloxanthops novemdentatus* was seen in the field feeding on sea urchins and small snails, snapping at shrimp, and trying to dislodge abalone, all of which may serve as food for the Xanthidae.

PREDATORS, PARASITES, AND COMMENSALS

PREDATORS

Brachyura. In the xanthid habitat, any of the brachyuran inhabitants are potential enemies, especially to the smaller xanthid individuals. Cannibalism and predation are common in the laboratory. On occasion smaller individuals are caught and eaten by members of the same species or by other species of the family Xanthidae. Within the family, however, predation is sporadic while herbivorous feeding is generally continuous. Whenever *Pachygrapsus crassipes* or *Cancer antennarius* is introduced into the aquaria it preys extensively on the smaller xanthid crabs.

On five occasions in the field between 2:00 AM and 6:00 AM *Pachygrapsus crassipes* was found feeding on soft, newly molted xanthid crabs. On one of these occasions two 20 mm *P. crassipes* were found with a 64 mm *Cycloxanthops novemdentatus* which they had just killed. At other times *Pachygrapsus crassipes* was found feeding upon the chelae of freshly molted crabs which had been severed at the breaking plane.

The secretive nature of the Xanthidae is probably their best defense against predation. All but the very large *Cycloxanthops novemdentatus* stay within a tunnel system between rocks, where they have a great deal of protection. There they can carry out all of their vital processes without leaving their niche.

Fish. While making periodic underwater observations, it was noted that the same habitat occupied by the Xanthidae is also occupied by blennioid fishes at high tide. These fish spend much of their time lying in wait on top of algal covered rocks. At times they were seen to dart from their hiding place and catch isopods. When small xanthid crabs were dropped nearby the fish made a serious effort to capture them. This suggests that the blennioid fish may be preying upon the xanthid crabs. To test this suggestion, stomach examinations were made on 51 blennioid fishes of the following species: 31 *Clinocottus analis* (Girard), 5 *Olygocottus maculosus* (Girard), 3 *Arteidius lateralis* (Girard), 5 *Gibbonsia eligans* (Cooper), and 7 *Gibbonsia metzi* Hubbs. The stomachs contained many limpets, snails, polychaetes, crustaceans,

and small fishes. Of the Crustacea there were isopods, amphipods, *Caprella*, stomatopods, shrimp, porcellanids, hermit crabs, and the following Brachyura: *Pachygrapsus crassipes*, *Lophopanopeus* spp., *Pugetia producta*, and *Herbstia* sp. In the stomach contents crustaceans were dominant, while mollusks were second in volume. Both adults and megalops of the genus *Lophopanopeus* were found, thus establishing the blennioid fishes as enemies of the Xanthidae. Limbaugh (1955) further substantiates fish as xanthid enemies when he states that *Paraxanthias taylora* is the favorite food of the Black Croaker in kelp beds, and that it is also eaten by Scorpionfish and Cabezon.

Snails. In March and April, 1955, numerous specimens of *Cycloxanthops novemdentatus* were found with small holes drilled in their exoskeletons. On close examination these holes appeared as those drilled in pelecypods by snails of the genus *Thais*. Two factors suggest this to be the work of a snail: (1) members of the genus *Thais* are often found in the xanthid zone, and (2) the xanthid crabs are inactive during the colder winter months and may easily fall prey to the oyster drill. Although experiments in the Foundation coldroom failed due to chemical contamination, circumstantial evidence and a comparison of drilled mollusk shells and crab exoskeletons direct suspicion to the snail. This condition was never encountered in the warmer summer months after the spring molt had occurred. The fact that drilled exoskeletons were found only during or after the coldest part of the year suggests that the inactive state of the crab aided the snail in its feeding.

The damage done to the xanthid crab is not very extensive. The hole becomes "plugged" by a blood-clot which turns black in a few days. Occasionally there is a discoloring of the exoskeleton around the hole, which suggests a secondary invasion by some organism. The fact that an appendage which is drilled is not autotomized further suggests that little damage is done to the crab.

Octopi. When the common octopus, *Octopus bimaculatus*, was kept with the Xanthidae in the laboratory it fed nightly on the crabs. An observation of this revealed that the octopus remained in hiding until a xanthid crab ventured out to feed. When this happened the octopus darted across the aquarium and caught the small crab in its tentacles. The little crab was then crushed and eaten. Although this act was never seen in the field, octopi were seen on three different occasions to swim out and catch small *Pachygrapsus crassipes*. The writer believes the octopus is no respecter of species and would readily capture a xanthid crab in the place of the grapsoid crab. Thus the octopus is considered an enemy of the Xanthidae.

PARASITES

The members of the family Xanthidae along the California coast are not heavily parasitized, though some cases of parasitism have been discovered in this study. Five nematode worms were found living in the

stomachs of four *Cyclozanthops novemdentatus*. These worms were large, tightly coiled individuals which occupied the area anterior to the gastric mill. It is not known if the relationship of these worms to the crabs was that of a parasite or a commensal.

Four possible species of rhizocephalan parasites were also found inhabiting various species of the Xanthidae. Boschma (1953) shows that only 12 species of Rhizocephala are known from the Pacific Coast of North America from the state of Washington to Alaska. A few of these have their ranges extended to Southern California, but no species whatsoever are known from Mexico to Central America. The few available records of xanthid parasites in Southern California are all from dredged specimens which came from essentially colder water. More data on this subject may show that the Xanthidae are generally free of parasites because they live in warmer zones which are "unfavorable" for the Rhizocephala.

The Rhizocephala are degenerate barnacles of the class Cirripedia. The free swimming larva attaches itself to a body "hair" of its crustacean host, and penetrates the base of that "hair" with its antennae. Then, after an interval of degenerative process, it enters its host by slipping through its own hollow antennae. Once inside, the rhizocephalan migrates into the body proper and resides in the region of the heart, stomach and liver. The parasite develops an extensive root system which penetrates every available haemocoelic space. The host molts only once after being infected. At this time the enlarged body of the rhizocephalan pushes through the soft body of its host in the region of the abdomen and develops its brood-sac externally.

The rhizocephalan, *Lorothyllacus panopaei* (Gissi.), was first named as a parasite of *Panopeus occidentalis* (Saussure). Later Boschma (1931) indicated the parasite of *Lophopanopeus b. bellus* from British Columbia to be this same species. The writer has discovered one rhizocephalan infection in *L. b. bellus* from Coos Bay, Oregon. This is a large bulbous parasite protruding through the abdominal wall of the crab. Rathbun (1930) also records a rhizocephalan parasite in *Lophopanopeus bellus diegensis* from Southern California. However, this specimen was not treated by Boschma (1950) in his study of Sacculinidae in the United States National Museum. The writer has also located two rhizocephalans attached to *L. b. diegensis* which were dredged off Redondo Beach, California. Superficially these look like *Drepanorhynchus tenuiculus* Boschma, but no taxonomic study of them has been made.

A third rhizocephalan was discovered in the body of *Cyclozanthops novemdentatus* while making a gonadal study. This parasite occupied a space dorsal and to the right of the heart. It extended anteriorly to the stomach, and posteriorly to the first abdominal segment. Strangely, the brood sac was full of developing embryos. This sac was very large, extending forward over the area of the right gonad, and was

thin and transparent, revealing the embryos within. Judging from written descriptions of other *Sacculina*, the location of the brood sac, and the state of embryo development, it seems unlikely that this individual would have completed its life history in the normal manner—with a brood-pouch extension through the host's abdominal mass. Therefore, this individual may be a new or different species from those already known.

Several cases of rhizocephalan infection of the genus *Thompsonia* were found on *Paraxanthias taylori*, *Lophopanopeus b. bellus*, and *L. b. diegensis*. *Thompsonia* is so lacking in taxonomic characteristics that only three species have been named in the Pacific. Reinhard (1944) published notes on some unnamed specimens from Washington that were attached to a hermit crab. Other records of this genus are lacking from the west coast of the United States.

Thompsonia differs in its life history from other rhizocephalans in that it produces numerous brood sacs as extensions of its root system. These develop beneath the exoskeleton of the body or limbs, and penetrate the new skeleton at the time of ecdysis. After penetration has occurred, larvae develop in the sacs, and are subsequently liberated. Unlike cases of other rhizocephalan infections the host can continue to molt and the parasite can develop new brood sacs (Potts 1915).

COMMENSALS

The Xanthidae of California are generally free of commensals. However, older individuals of the three major genera, especially *Cyclozanthops novemdentatus* and *Paraxanthias taylori*, may support many commensals. There are several explanations for this occurrence: (1) young individuals molt very frequently and thus cast off any commensals, whereas older crabs have more time between molts to accumulate commensals; and (2) older crabs are occasionally less active and continually inhabit niches where their commensals are commonly sessile in the habitat of the Xanthidae. Thus, there is no peculiar association of animals, but rather a normal incidence of sessile animals which settled upon crabs rather than a rock or alga.

The most common commensals are two species of sinistral and two species of dextral *Spirorbis* (*Polychaeta*). These settle on the carapace, abdomen, external mouth parts, walking legs, or chelipeds. Another common commensal is a bryozoan, *Cauloramphus spiniferum* (Johnson), which settles and grows on any exposed surface. Two genera of sponges, *Aletes* and *Plocamia*, are found occasionally growing on the leg bristles of *Paraxanthias taylori*.

At no time were commensals found to interfere with the movement of articulating body parts. Occasionally a great number of *Spirorbis* were found on the maxillipeds which may have caused some interference with feeding activity. Other than this, however, commensals seem to have no unfavorable effect on their hosts.

ECONOMIC AND FUTURE STATUS OF THE XANTHIDAE OF CALIFORNIA

The crab fisheries, which are of considerable economic importance in the United States, are dependent on a ready source of meat-producing crabs that can be obtained in large quantities for market. These crabs are either trapped or dredged commercially, or netted by sportsmen.

None of the Xanthidae of California is suitable for such purposes. Aside from *Cycloxanthops novemdentatus*, the largest individuals recorded measure no more than 45 mm across the carapace. While large *C. novemdentatus* may measure 80-95 mm, they will weigh only about 0.25 lb. The claws of this species are of fair size, but the legs, as compared with a "meat crab," are very small. Then too, this species would have to be gathered by hand or trapped, as the nature of its habitat would make a dredge useless. The effort necessary to trap these crabs in the intertidal areas along rocky beaches would not be repaid by the catch obtained.

The meat of *Cycloxanthops novemdentatus* has a delicate flavor which compares very favorably with that of market crabs. However, the segments of meat are very small, and the effort involved in obtaining them is considerable. The body and legs require careful cracking and picking. Once removed, the meat can be salted or prepared in a salad and eaten.

The adult and larval Xanthidae probably contribute, in a minor way, to food chains of fishes and other animals, including such important market fish as herring and mackerel. Aside from this, however, they should be considered as being of no economic importance.

The future of the Xanthidae in California is not a clear one. The apparent absence of *Pilumnus spinohirsutus* (a minor member of the California Xanthidae), especially in its northern range, as well as the dearth of *Cycloxanthops novemdentatus* and *Paraxanthias taylora* at their northernmost range, suggests a very slow southern shift of range. On the other hand, the recent appearance of *Rhithropanopeus harrisi* in San Francisco Bay, California, and Coos Bay, Oregon, balances the possible loss of *Pilumnus spinohirsutus*.

Public abuse of the California beaches may pose a new threat to the Xanthidae and to other intertidal animals as well. Along the Palos Verdes cliffs such abuse can be seen in two forms. First, skin divers and, more commonly, non-swimming abalone collectors and others, continuously overturn the rocks which overlie the substrate along the cliffs; few of the rocks are ever turned back. This means that animals and plants which are normally exposed to open wave action, or the reverse—animals and plants which are normally on the protected under side of the rock, are left in unfavorable oceanographic conditions. Consequently many individuals in a finely balanced intertidal habitat die out, and the decrease in the total population of the species is felt by the other inhabi-

tants. In time, however, many forms are replaced by settling larvae or spores which attach and grow on the newly vacated surfaces. Secondly, many of the rocky beaches are being littered with cans, bottles, all sorts of junk, and even old automobiles which are dumped off the cliffs or left on the beach. Much of this material decomposes in or out of the water and may make conditions somewhat less favorable to marine life. Alongshore current systems constantly exchange the tidepool water, thus preventing a high, toxic concentration of decomposed material. Indirectly, pollution is blamed for the dearth of algae at Point Fermin which, in turn, is responsible for reduced animal populations there.

Any factors which make the water toxic, or reduce the microscopic algae, are likely to affect the xanthid population. New housing developments along the cliff-edge at Palos Verdes are making the shore less accessible to the public. This, as well as the scheduled improvements in sewer outlets, may reduce habitat destruction, the dumping of refuse, and pollution, thus enhancing the chances for survival of the Xanthidae of California.

SUMMARY

1. The family Xanthidae is primarily of tropical waters but is represented in California by five genera and seven species. Of these, *Lophopanopeus leucomanus leucomanus* (Lockington), *Lophopanopeus bellus diegensis* Rathbun, *Paraxanthias taylora* (Stimpson), and *Cycloxanthops novemdentatus* (Lockington) are most abundant intertidally along the coast and thus are considered the major forms.

2. Sites for field studies were located at Palos Verdes and Corona Del Mar, California, while collections and field observations were made from Oregon, in the north, to Baja California, Mexico, the Gulf of California and the Tres Marias Islands, Mexico in the south.

3. The Xanthidae were found to dwell in three types of habitats all along the California Coast. These are found to be very similar in physical structure to the tropical habitats occupied by the pebble crabs.

4. The basic habitat type (Habitat One) consists of large, protected rocky beach tidepools which are generally guarded by rocky reefs or series of very large rocks. Reefs and nearby rocky headlands reduce wave action. The bottom of such pools is covered with several layers of large rocks, cemented together with algae and encrusting animals. A turf of coralline algae and *Colpomenia* serves as an indicator. This habitat provides a solid substrate, a network of small hiding places, ample algae for food, protection from predators and wave action, and good water circulation. This habitat closely resembles the coral-head habitat of the tropics. Adults of *Paraxanthias taylora* and *Cycloxanthops* along with a few juveniles of the three major genera are found here.

5. The second type of habitat (Habitat Two) resembles the first in that rocky headlands afford protection from waves but differs in that there are fewer

large rocks for protection, hence heavier surf action. The substrate consists of a single layer of rock-over-sand or a solid sheet of bedrock. A turf of *Gigartina* serves as an indicator of this habitat. This habitat has the same physical characteristics as many rock-over-sand or bedrock habitats found inshore from outlying coral reefs in the tropics. *Lophanopeus l. leucomanus* and juveniles of *Cyclozanthops novemdentatus* are common here.

6. The third type of habitat (Habitat Three) is found within the mouth of protected channels. It consists of rock on sand, or rocky channel walls with tube snail colonies offering hiding places. Oceanic waves are totally lacking, being replaced by less significant waves produced by boat movements. *Lophopanopeus bellus diegensis* is most common here while juveniles of *Cyclozanthops novemdentatus* and juveniles and adults of *Paraxanthias taylora* are in smaller numbers.

7. Both juveniles and adults of *Cyclozanthops novemdentatus* and *Lophopanopeus* spp. dwell primarily between the lower sand or pebble substrata and the first layer of overlying rocks. *Paraxanthias taylora* juveniles and adults show preference in dwelling well up above the lower sand substrata just below the top layer of rock.

8. Xanthid crabs commonly move sideways but can walk directly forward or backward. In backward locomotion the last pair of walking legs is raised as "feelers." When some object is contacted the last pair of legs "walks" along the vertical wall of the object, thus guiding the crab along its contours. Within a small rock crevice the last pair of legs is pressed against the ceiling while the other legs remain on the floor. By extending the legs the crab wedges itself in and thus can move about even in heavy wave action.

9. Xanthid crabs resort to a "freeze response" which may be triggered by a sudden change in light intensity, visible movement, or mechanical disturbance, or all three together, but probably depends on the degree of activity prior to being exposed.

10. The xanthid eye is quick to detect any slight movement, though the typical reaction, the freeze response, would not tend to emphasize this.

11. Hiding places are quickly found by xanthid crabs within the tidepool habitats. The places consist of small crevices or spaces under rocks and are located solely because they appear as dark places and not because the physical contours can be determined by the crabs.

12. Xanthid crabs apparently recognize some possible food items such as living snails, but the exact means of recognition may not be visual.

13. As with other crabs, xanthid crabs display a compensatory movement of the eyes, in which the plane of the eye tends to remain the same while the body rotates.

14. The sensation of the legs against a solid substrate is a requisite for orientation. When this is

fulfilled the visual and balance centers take over but are probably secondary in this matter.

15. The California Xanthidae are essentially herbivorous, secondarily scavengers and thirdly predators. Food is located by the chemical, visual, and tactile senses functioning as an integrated unit or individually as the type of food or environmental circumstances demand.

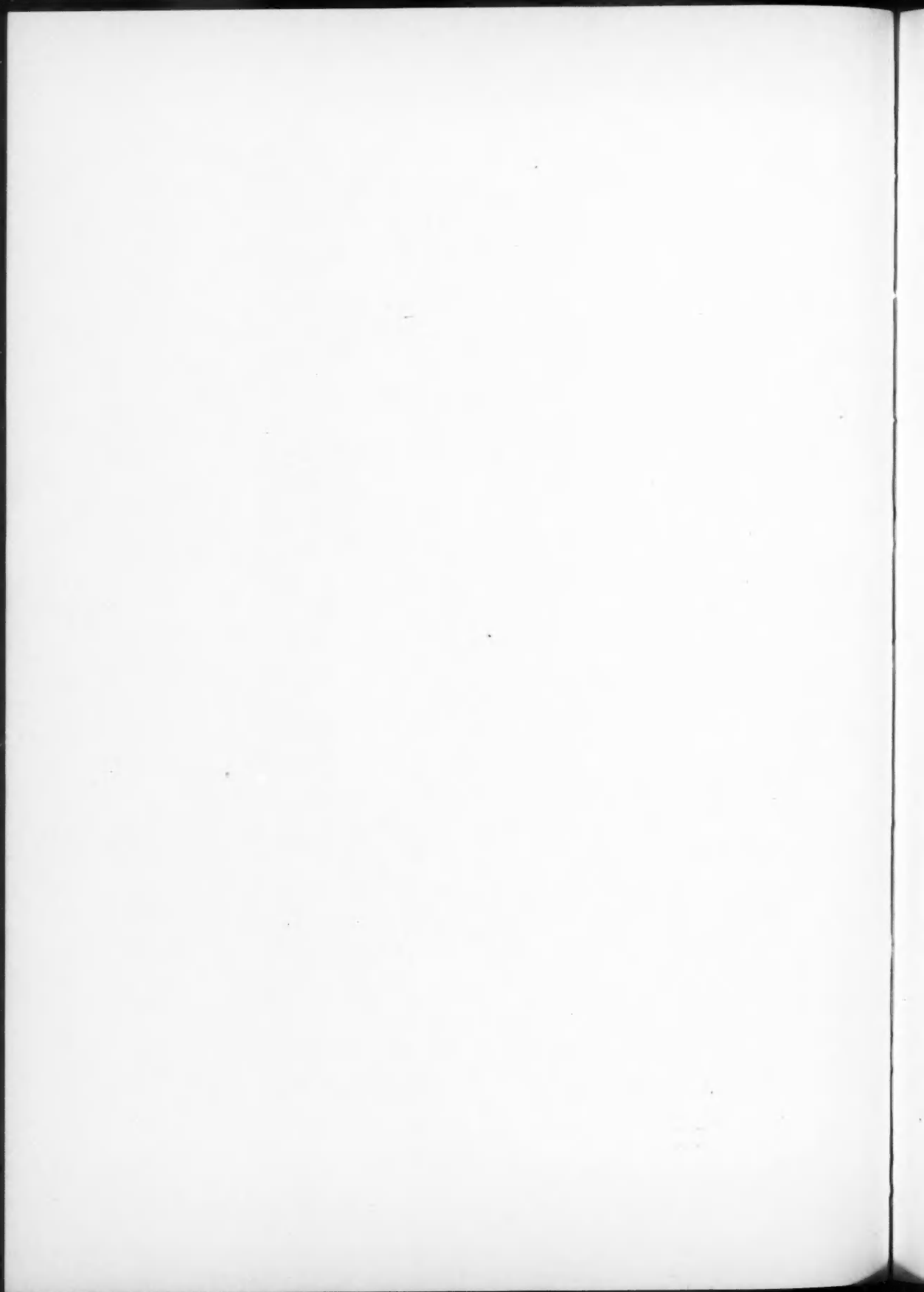
16. The enemies of the Xanthidae are crabs, fish, snails, and octopi; they have few parasites (primarily rhizocephalans, if any), but may harbor many commensals when the period between molts is long.

17. The future status of the California Xanthidae is not clear. Skin divers and public abuse of some beaches pose a threat to the crabs. One species may now be absent while a new species has recently been recorded in California. Aside from the larvae being used by plankton feeders, the xanthid crabs are of no economic importance.

LITERATURE CITED

- Andrews, C. W. 1909. On the robber crab (*Birgus latro*). Proc. Zool. Soc. London 79(2): 887-889, pl. 1.
- Bethe, A. 1896. Ein Beitrag zur Kenntnis des peripheren Nervensystems von *Astacus fluviatilis*. Anat. Anz. 12: 31-34.
- . 1897. Das Nervensystem von *carcinus maenas*. Arch. f. Mikros. Anat. 50: 460-546, 589-640.
- Boschma, H. 1931. Rhizocephala. Papers Mortensen's Pac. Exp. 1914-1916, L. V. Vidensk. Medd. Dansk. Naturk. Foren. 89: 20-21.
- . 1950. Notes on Sacculinidae, chiefly in the collection of the United States National Museum. Zool. Verh. 7: 1-55, figs. 1-35.
- . 1953. The Rhizocephala of the Pacific. Leyden Rijks Mus. van Nat. Hist. Zool. Meded. 32(17): 185-201.
- Clark, G. P. 1896. On the relation of the otocysts to equilibrium phenomena in *Gelasimus pugilator* and *Platyonichus ocellatus*. Jour. Physiol. 19: 327-334, figs. 1-5.
- Cott, H. B. 1929. Observations on the natural history of the Racing Crab (*Ocypoda ceratophthalma*) from Beira. Proc. Zool. Soc. London 99(2): 755-765, figs. 1-2.
- Cowles, R. P. 1908. Habits, reactions, and associations in *Ocypoda arenaria*. Carnegie Inst. Wash., Dept. Mar. Biol. Papers 2(1): 3-41, figs. 1-10.
- Garth, J. S. 1946. Littoral brachyuran fauna of the Galapagos Archipelago. Allan Hancock Pacific Exped. 5(10): 341-600, text fig. 1, pls. 49-87.
- Hara, S. L. 1933. A note on the bionomics of two estuarine crabs. Proc. Zool. Soc. London 103(2): 881-884, figs. 1-6.
- Hiatt, R. W. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pac. Sci. 2(3): 134-213, figs. 1-18, tables 1-12, pls. 1, 2.
- Knudsen, J. W. 1957. The act of molting in the California Xanthidae, the pebble crabs. Bull. South. Calif. Acad. Sci. 56(3): 133-142, pls. 28-30.
- Limbaugh, C. 1955. Fish life in the kelp beds and the effects of kelp harvesting. Univ. Calif. Inst. Mar. Res. La Jolla, Calif., I. M. R. Reference no. 55-9.

- List, T. 1897. Morphologisch-biologische Studien über den Bewegungsapparat der Arthropoden. Mitt. Zool. Sta. Neapol. 12: 74-168.
- Lyon, E. P. 1899. A contribution to the comparative physiology of compensatory movements. Am. Jour. Physiol. 3: 86-114, figs. 1-3.
- Menzies, R. J. 1948. A revision of the Brachyuran genus *Lophopanopeus*. Allan Hancock Pubs. Occas. Paper 4: 1-45, pls. 1-6, 3 graphs.
- Milligan, H. N. 1915. The habits of the Four-horned Spider Crab. Zoologist, 4th ser. 19: 245-256, figs. 1, 2.
- Nagel, W. A. 1894. *Vergleichend physiologische und anatomische Untersuchungen über den Geruchs- und Geschmackssinn und ihre Organe mit einleitenden Betrachtungen aus der allgemeinen vergleichenden Sinnesphysiologie*. Bibl. Zool. pp. 1-207.
- Pearse, A. S. 1931. The ecology of certain crustaceans on the beaches at Misaki, Japan, with special reference to migrations from sea to land. Elisha Mitchell Sci. Soc. Jour. 46(2): 161-166, pl. 11.
- Potts, F. A. 1915. On the Rhizocephalan genus *Thompsonia* and its relation to the evolution of the group. Carnegie Inst. Wash. 8(1): 1-32, pls. 1, 2, figs. 1-12.
- Rathbun, M. J. 1930. The canceroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Canceridae, and Xanthidae. U. S. Nat. Mus. Bull. 152: 1-193, pls. 1-230.
- Reinhard, E. G. 1944. A hermit crab as intermediate host of *Polymorphus* (Acanth.). Jour. Parasit. 30(3): 201.
- Schmitt, W. L. 1921. The marine decapod Crustacea of California. Calif. Univ. Pubs. Zool. 23: 1-470, text figs. 1-165, pls. 1-50.



ENERGY DYNAMICS OF A FOOD CHAIN OF AN OLD-FIELD COMMUNITY

FRANK B. GOLLEY

Department of Zoology, Michigan State University, East Lansing, Michigan*

TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	187	Production of Young by Adults	197
Description of the area	187	Production of Tissue	198
METHODS	188	Immigration into the Study Area	199
Measurement of Solar Insolation	188	Respiration of the Mouse Population	200
Studies of Vegetation	189	Summary of <i>Microtus</i> Energy Assimilation	200
Studies of the <i>Microtus</i> Population	189	Digestibility of Food	200
Studies of the Least Weasel	193	Consumption of Food	200
RESULTS	193	The Least Weasel Population	202
Solar Energy	193	DISCUSSION	203
Dynamics of the Vegetation	194	Energy Losses of the First Order	203
The Dynamics of the <i>Microtus</i> Population	196	Energy Losses of the Second Order	204
Standing Crop of <i>Microtus</i>	196	SUMMARY	204
Caloric Value of <i>Microtus</i> Tissue	197	LITERATURE CITED	205
Mortality or Emigration of Mice	197		

INTRODUCTION

In recent years there has been a growing interest in the study of the transfer of energy through natural systems (ecosystems, Tansley 1935). Park (1946) stated that "probably the most important ultimate objective of ecology is an understanding of community structure and function from the viewpoint of its metabolism and energy relationships." Aquatic biologists have taken the initiative in the study of community energetics, and most of the information available today concerns fresh water or marine communities. A great need exists for similar studies on terrestrial communities.

In this study a food chain of the old field community, from perennial grasses and herbs to the meadow mouse, *Microtus pennsylvanicus pennsylvanicus* Ord, and to the least weasel, *Mustela vison allegheniensis* Rhoads, was chosen for investigation. This food chain included the dominant vertebrate of the community (*Microtus*) and one of its main predators (*Mustela*) but excluded the otherwise important insects, other invertebrates, bacteria, and fungi. The primary objectives of the study were to determine (1) the rate of synthesis of organic matter by the primary producers—the vegetation, (2) the path of this energy from the vegetation through the mouse to the weasel, and (3) the losses of energy at each step in the food chain.

The writer wishes to acknowledge with gratitude the suggestions and guidance of Dr. Don W. Hayne, Institute of Fisheries Research, Michigan Department of Conservation, especially concerning that portion of the study dealing with the population dynamics and productivity of the *Microtus* population. The writer also thanks Dr. John E. Cantlon, Department of

Botany, and Dr. Robert C. Ball, Department of Fisheries and Wildlife, Michigan State University, for aid given throughout the project. The investigation was supported by the Michigan Agricultural Experiment Station through a project administered by Dr. Hayne.

DESCRIPTION OF THE AREA

The study area was located in a large field on the Michigan State University State Farm approximately one mile south-east of Okemos, Ingham County, Michigan (sec. 27, T. 4N, R. 1W). As far as is known, this farm was last tilled in 1918 when it was given to the State of Michigan by Mr. John Fink. It was acquired by Michigan State University in 1940 and was pastured from 1940 to 1942. The study area has been undisturbed since 1942, with the exception of some tree planting by the Department of Forestry, Michigan State University, and probably occasional burning. The tree plantings appeared to be only slightly successful. The vegetation on the area was unburned from January 1952 to March 1957.

The field in which the study area was located was situated on the north terrace of the Red Cedar River, approximately 20 ft above the level of the river. The topography was gently undulating, with a relief of 15 ft or less. A shallow depression ran through the center of one of the trapping areas and served as a drain during the heavy rains in the winter and spring. On February 9, 1957, the snow melt-water was approximately 7 in. deep in this drainage area. As the snow melted in February and March much of the study area was inundated, with grass hummocks and hillocks on the border of the trap area providing the only dry sites.

The soils on the study area were predominantly Conover and Miami loam (determined from the soil map by Veatch *et al.* 1941).

* Present Address: Department of Zoology, University of Georgia, Athens, Georgia.

On the east the field was separated from similar habitat by a paved county road. The north boundary was predominantly pasture land and orchard. The west boundary was an experimental alfalfa field left uncut in 1957. To the south the field was bounded by an unused gravel road, which ran along the ridge top above the river terrace and separated the field from other old field vegetation containing more woody cover and indicating a later stage of old field development. The field itself contained approximately 10 ha of relatively homogeneous habitat.

The climate in this area of Michigan is characterized by cold winters and mild summers (Baten & Eichmeier 1951). Yearly precipitation at East Lansing (1911-1949) averages 31 in.; growing season (last day in spring to the first day in fall when the temperature reaches 32°F) precipitation averages 17 in. The mean annual temperature is approximately 47°F, with extremes ranging from -20° to +102°F. The growing season averages 147 days. Solar radiation at East Lansing (3 mi west of the study area) is peculiar in that a plateau in the insolation curve may be expected about April 25 to May 20. When solar energy received at East Lansing is compared with that at most of the 92 weather stations in North America measuring solar insolation, it is evident that East Lansing receives annually less solar heat than any other station, with the exception of Fairbanks, Alaska (Crabb 1950b).

No attempt was made to make a complete survey of the flora and fauna of the community. The vegetation of the study area was transitional between the perennial grass stage (perennial grasses predominant) and the perennial herb stage (perennial herbs co-dominant with the grasses) of old field succession (Beckwith 1954). The vegetation is considered similar to the bluegrass-upland association of Blair (1948) and the upland community of Evans & Cain (1952).

Canada blue grass, *Poa compressa*¹, was dominant over the entire area, with three herb species, *Daucus carota*, *Cirsium arvense*, and *Linaria vulgaris*, sharing dominance in portions of the area. The study area was divided into four facies on the basis of co-dominance of the above herbs with *Poa compressa*. Mosses, undeveloped small herbs, and grass shoots formed a subordinate layer beneath the grass and perennial herb layer. A woody overstory occurred sporadically over the area, consisting primarily of *Crataegus* spp., *Pyrus communis*, *Prunus pennsylvanica*. The woody plants were a relatively unimportant component of the vegetation, the percentage cover for all woody plants averaging approximately 0.5.

The vertebrate dominants of the community, excluding birds, were *Microtus pennsylvanicus* and *Blarina brevicauda*, when total number observed was used as the criterion of dominance.

¹ Authorities for vascular plant binomials are those given in Fernald (1950).

METHODS

As energy flows through a terrestrial food chain there is a successive transfer and loss of energy at each step in the chain (Fig. 1). As a result of the continual loss of energy through respiration and through nonutilization of food, each successive population is faced with a smaller energy source. In this report the writer's approach has been to study the energy flow through each separate population, rather than to emphasize the energy exchange through the food chain as a whole. In the traditional style of presenting research methods and results separately, this concern for each species population becomes especially evident and necessarily obscures the picture of energy flow through the entire food chain. The writer believes that this method of presentation is most satisfactory for an exploratory study of this nature. However, by referring to Fig. 1, the reader will be able to follow the flow of energy through the food chain without difficulty.

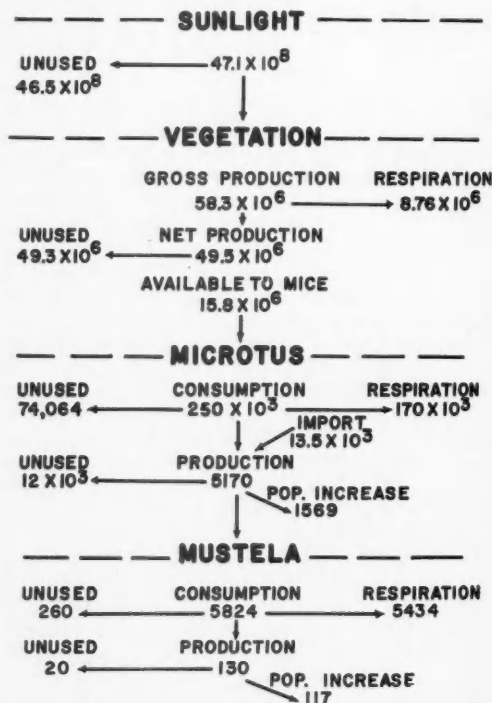


FIG. 1. The energy flow through the food chain from May, 1956 to May, 1957, on one hectare. All figures are Calories per hectare. Solar input represents that for the 1956 growing season.

MEASUREMENT OF SOLAR INSOLATION

Records of solar insolation (the rate at which solar energy is received on a horizontal surface at the surface of the earth) were obtained from the Michigan Hydrologic Research Station (the Agricultural Research Service, USDA, and the Michigan Agricultural

Experiment Station cooperating). The station operates an Eppley ten-junction thermopile, thermoelectric pyrliometer, mounted on a small instrument house on an isolated section of the Michigan State University Farm, East Lansing. There is little smoke contamination at this location (Crabb 1950a) and it is assumed that the records obtained at the pyrliometer were applicable to the study area approximately 3 mi to the east.

STUDIES OF VEGETATION

The vegetation was studied from August 1956 to September 1957. Midway through the investigation (March 1957) a fire destroyed the vegetation on one-half of the study area, and it was necessary to move the entire operation to another portion of the same field. Fortunately there was no discernible difference in vegetation or topography at these two locations.

Square clip-plots (0.5×0.5 m) were used to estimate the standing crop of vegetation. All plant stems within the quadrats were clipped at the ground level. The cut vegetation was transferred to plastic bags and transported to the laboratory, where live grasses, live herbs, and dead vegetative materials were separated according to species. These materials were then dried at 100°C for 24 hrs and weighed. Monthly data were averaged and the standing crop of vegetation was expressed in grams of dry weight per 0.25 m^2 . Ten to twenty random clip-plots were chosen for investigation each collection period, with the exception of late March. The adverse weather conditions in the latter part of March allowed an estimate to be made of green vegetation on only two plots.

Samples of several months' collections of dried grasses and herbs were randomly chosen for calorific analyses. These materials were ground in a Wiley Mill. Three subsamples from each species sample were analyzed in a Parr adiabatic bomb calorimeter.

The standing crop of roots and above-ground portions of the plants which escaped clipping were also determined at three periods during the 1957 growing season. At each collection, five of the plots which had been clipped were chosen at random and a 225-cm^2 piece of sod was cut from each plot. The sod was later washed in running water, oven dried at 100°C and weighed to determine average weight of roots per square meter. The samples were taken to a depth of 15 cm and did not represent the complete root biomass. Although Shively & Weaver (1939) show that the roots of many prairie plants extend at least several feet into the soil, for this study it was assumed that the main mass of roots in the old field community were concentrated within 15 cm of the surface.

The standing crop of vegetation measured here was less than the total amount of organic matter synthesized over the growing season. This is because the standing crop includes neither the amount of vegetation which grew and died between the periods of measurement, nor the amount of vegetation consumed

by animals. In this study, some dead vegetation of the current growing season was unavoidably included with the green vegetation since no effort was made to separate the dead and living portions of one leaf or small plant. The material that grew and died back to the ground during the current growing season could not be separated from the dead vegetation and is therefore a source of error in determination of net production. The magnitude of this error was not estimated.

The amount of vegetation consumed by *Microtus* was estimated from feeding experiments and stomach sample analyses. The food consumption of herbivorous insects and other invertebrates, which in the pasture community may be of considerable magnitude (Wolcott 1937), was undetermined.

Another source of error in estimating the net production of the vegetation is pointed out by Pearsall & Gorham (1956). They suggest that in perennial vegetation the peak standing crop is formed from (1) the accumulation of the organic matter during the present season and from (2) the organic matter stored in the roots the previous season. The techniques used in this study allowed no estimate of the contribution of the previous season's production to the current peak standing crop.

To obtain a complete estimate of the energy utilization of vegetation (gross production, Odum 1956), the energy used in respiration of the vegetation must be added to the net production. A field respirometer was devised to make a rough measure of the respiration of the vegetation and the soil organisms. Two 5-qt oil cans were forced 5 cm into the ground at randomly chosen sites on the study area. Gases were withdrawn from the cans into Bailey gas analysis bottles. Carbon dioxide and oxygen content of the air in the cans was determined in an Orsat-Henderson gas analysis apparatus. The cans were placed in the ground and the first samples were withdrawn approximately 1 hr after dark. The second sample was taken in the early morning when the air temperature at the ground surface was approximately equal to the air temperature observed when the first samples were withdrawn the previous night. The consumption of oxygen and production of carbon dioxide over the night (12 hrs) was determined as the differences in the percentage composition of oxygen and carbon dioxide in the air in the cans at the first and second sampling. No measurement was made of the diffusion of gases between the soil and the air under the cans. The RQ (CO_2/O_2) was calculated and the thermal equivalent (in Calories) of the oxygen used and the carbon dioxide produced was extrapolated from the tables in Brody (1945). Respiration was then expressed as Calories used per gram of plant tissue per hour respiration during the night.

STUDIES OF THE *Microtus* POPULATION

The energy dynamics of the *Microtus* population were studied both in the field and by laboratory experiments. In the field a live-trapping program was

TABLE 1. Dynamics of the *Microtus* population on one hectare

Date	Average Number Captured Per Line	Fraction ¹ Per cent	Population Density Per Hectare Numbers	Size of Trap Area Hectares	Average Individual Weight Grams	Standing Crop per Hectare Calories ²	MORTALITY BETWEEN SUCCESSIVE TRAPPING PERIODS	
							Rate ³	Calories
May 22-28.....	4	29.4	5.2	2.6	29	205	75	393
July 24-30.....	12	41.7	9.6	3.0	29	382	37	232
Sept. 4-10.....	20	41.0	16.5	3.0	29	654	52	539
Oct. 9-15.....	19	32.4	21.2	2.7	31	898	42	710
Nov. 17-23.....	28	22.2	42.4	2.4	29	1685	39	1162
Jan. 6-23.....	22	(13.3) ⁴	77.3	2.1	27	2847	27	1245
Feb. 21-27.....	39	13.0	139.1	2.1	29	5525	(55) ⁴	3284
March 19-26.....	22	13.6	75.3	2.2	25	2578	35	937
April 25-1.....	43	30.4	53.2	2.6	32	2330	57	1931

¹ The percentage of total captures taken in common to both lines.² Caloric value of *Microtus* was 1.37 Calories per gram.³ Percentage disappearing from one trap period to the next.⁴ Estimated values.*

initiated in May 1956 and continued to September 1957. This paper includes only the data for one annual cycle, May 1956 to May 1957. The program was designed to yield information on population density, mortality, growth rate, and production of young. The trapping design was developed by D. W. Hayne and consisted of two crossed trap lines, 100 m long, with the live traps spaced 2 m apart. One trap line was operated for 24 hrs, it was then unset and the line crossing it was set for 24 hrs. The total trapping period extended for 6 days, with 3 days for each line. Since by the sixth day of trapping unmarked animals were generally caught only in the end traps in a line, it was assumed that six days of trapping was adequate to capture most of the animals living in the trap area. It was desirable to use as short a trapping period as possible because trap mortality tended to increase progressively during the trapping period.

Captured animals were toe clipped, sexed, aged, weighed, and examined for breeding condition before being released. Traps were baited with oatmeal, and during the colder months corn was also placed in the traps to serve as a high energy supplement. It was thought that the use of corn materially reduced trap mortality during the winter. Covers, made of asphalt shingles covered with aluminum foil, shielded the traps from sunlight, rain, and snow and were thought to reduce trap mortality especially in the summer.

A ratio method was used to estimate population density. The following formula was suggested by D. W. Hayne:

$$P = \frac{bc}{ad} \quad (1)$$

where a is the number of animals captured in common to both lines, b the average number of animals captured in each of the two lines (both a and b exclude those animals dying in the traps during the trapping period), c average for the two lines of all captures including deaths due to trapping, d the effective area trapped, and P the population density per unit area.

The trap area, bisected by each trap line, was a square of 10,000 m². Since the home ranges of the mice extended an unknown distance beyond these lines the square was increased on both sides and ends. On each side the area added was set arbitrarily as

the fraction $\frac{a}{b}$ (in Formula 1) times one-half the trap line length, 50 m, times the length of one side, 100 m. At each end of the trapping square, the area was increased by a semicircle with a radius of one-half the length of the trap line plus the fractional increase computed above. Information on numbers captured and population estimates are shown in Table 1.

In calculating the production of (or total weight grown by) the *Microtus* population, it was necessary to use one method for the animals which were susceptible to capture (the adults and an unknown proportion of the juveniles) but to use an entirely different method for the nestling young which do not enter traps. For the trapped animals, production was calculated from the rates of growth and mortality observed among the trapped individuals, while for the nestling young, production was inferred from the observed rate of pregnancy, the known rate of growth of young, and the calculated rate at which the young entered the trap-susceptible population.

In calculations of production, the use of instantaneous rates has been advantageous (Clarke 1946, Clarke Edmondson & Ricker 1946, Ricker 1946). Assuming constant rates, the products of the instantaneous rates and the mean population for a period will yield, respectively, the production of animal tissue by the population and the quantity of tissue lost from the population. This approach is especially useful here since it allows estimation of the biomass or number of animals which were produced, grew, and were lost between measurements of the standing crop.

The recapture of resident animals in two consecutive trapping periods allowed an estimate to be made of the rate of weight gain or loss of the individuals.

This rate was estimated separately for the animals in a number of 10-gm weight classes, since the rate of growth changes with body weight (Table 2). For each weight class, the daily instantaneous rate of growth was multiplied by the mean biomass for the period to calculate the daily production by growth or the daily weight loss in that particular weight class. A proportionate weight change of less than one indicated that the animals in that class lost weight (Table 2).

To determine the production of the nestling young, it was necessary to establish (1) the potential production of young by the population (potential natality), (2) the number of young which entered the trap-susceptible population, and (3) the growth rate of the young. The estimate of the potential production of young was based on the rate of pregnancy determined in the field and on the gestation period and litter size as reported in the literature. Pregnancy rates were established by abdominal palpation of all females. Davis (1956) suggests that pregnancy is "visible" for 18 days in small rodents—this would mean that 86% of the pregnancies could be determined by abdominal palpation. Although Davis's findings could probably be extended to *Microtus*, the percentage of adult females found to be pregnant in this study (Table 3) was so large during most of the breeding season that Davis's correction could not be made. The average number of days required for a female in the population to produce one litter can be found by dividing the gestation period (21 days, Hamilton 1941) by the proportion of females pregnant, here termed f . With the additional assumptions that there is an even sex ratio and an average of five young per litter (Hamilton 1941, Hatt 1930, Blair 1940), we can infer that in each time interval of $21/f$ days, one female increases to 3.5 females—2.5 young females plus the mother. With the use of the following formula it is then possible to calculate the production of young:

$$\frac{\text{nat log } 3.5}{\frac{21}{f}} \times t \times p' \quad (2)$$

where f is the percentage pregnancy among females, t is the time between trapping periods, and p' is the mean population.

The number of young entering the trap-susceptible population was assumed to equal the number of adults and juveniles lost to mortality plus the number needed to fulfill the population increase.

The growth rate of the nestling young was based on the weight increase from an assumed birth weight to the weight of the lightest juvenile captured in the live traps between trapping periods. Whitmoyer (1956) showed that the mean birth weight of laboratory *Microtus pennsylvanicus* was approximately 3 gm. The lightest weights of live-trapped juveniles ranged from 10 to 16 gm. The products of the instantaneous rate of growth of the nestling young and the mean biomass of young yielded the increase

TABLE 2. Tissue production of juveniles and adults per hectare.

Interval	PROPORTIONATE WEIGHT CHANGE WEIGHT CLASSES IN GRAMS				DAILY INSTANTANEOUS RATE OF GROWTH ¹		Growth Calories	Weight Loss Calories
	11-20	21-50	31-40	41-50	+	-		
May.....	data not available							
July.....	data not available							
Sept.....	2.06	1.00	1.10	—	3.08	—	74	—
Oct.....	1.86 ²	1.20	1.00	.96	3.03	.19	81	5
Nov.....	1.70	1.04	.82	.69	1.32	2.28	56	95
Jan.....	—	.99	.86	—	—	5.15	—	123
Feb.....	—	—	.94	—	—	8.20	—	152
March.....	1.71	1.27	.99	.91	20.92	.68	516	17
April.....	1.87	1.21	1.03	.91	9.92	1.72	190	33

¹ Positive and negative daily instantaneous rates of growth derived from proportionate weight gains and losses of all weight classes within the month.

² Boldface growth rates were calculated by the increment method.

TABLE 3. Potential production of new *Microtus* per hectare.

Date	Time Interval Between Trapping Days	Pregnancy Rate Per Cent	Mean Adult Population Numbers	POTENTIAL PRODUCTION	
				Numbers	Calories
May.....	64	90	7.2	24.8	102
July.....	42	90	12.6	28.5	117
Sept.....	35	90	18.5	34.8	143
Oct.....	39	90	30.7	64.5	265
Nov.....	61	65	58.2	137.9	567
Jan.....	35	00	104.7	—	—
Feb.....	27	60	103.7	—	—
March.....	36	11	63.5	15.2	63
April.....	28	92	51.5	79.3	326
Totals.....				385.0	1583

in mouse tissue due to the nestlings between the two trapping periods. The contribution of nestling young is shown in Table 4.

TABLE 4. Growth of nestling young per hectare.

Date	Mean Biomass Grams	Growth Rate	TOTAL GROWTH	
			Grams	Calories
May.....	144	5.33	242	331
July.....	135	5.33	226	309
September...	180	5.33	302	414
October.....	333	4.67	516	706
November...	893	7.67	1231	1686
March.....	100	4.67	154	211
April.....	361	3.30	435	596
Totals....			3106	4253

When the amount of energy leaving the *Microtus* population through respiratory processes is added to the production of tissue, the result is a measure of the assimilation of the population. Assimilation is defined here as the energy which enters the population and is actually used in productive or maintenance processes. An estimate of the respiratory energy loss was made by studying the metabolic rate of *Microtus*

by the McLagan-Sheahan (1950) closed circuit method. This technique utilized a series of desiccator jars connected to a pure O_2 source, a vacuum pump, and mercury manometers. Soda lime, in the bottom of jars, absorbed CO_2 . The system was of known volume (approximately 2600 ml) and was kept at a constant temperature of $26^\circ C$. Wild *Microtus* were trapped the day before the experiment and fasted over night (12 hrs). Three or four mice of the same sex and weight were placed in each jar and, after air was evacuated from the jars to a negative pressure of 200 mm Hg, pure O_2 was introduced until pressure returned to equilibrium. As the O_2 was consumed in the jars, the pressure changes were measured on mercury manometers. The mice were allowed about 30 min to become accustomed to the apparatus before readings were made on the manometers. After this initial period, the mice were maintained in the jars for 1 hr. A respiratory quotient (RQ) of .85 was assumed in the computations of metabolic rate.

Metabolic rate determined by this method can not be considered a basal rate (BMR) because the animals were slightly active in the jars during the experiments. Rather than basal rate, this study determined the fasting metabolic rate (FMR) of *Microtus*. The FMR (Table 5) was calculated in terms of cc of O_2 consumed per gm mouse tissue per hour and in Cal per 24 hrs per individual mouse. The respiration of the adult biomass was estimated by multiplying the metabolic rate in Cal per 24 hrs per mouse by the population density at a trap period and by the number of days between succeeding trap periods. The product of the metabolic rate of the young (assumed to be 1.7 Cal per 24 hrs), the mean population of young, and the time interval between trapping periods yielded the respiration of the nestling young.

TABLE 5. Respiration of experimental animals.

Date	Ave. Weight Individuals Grams	Oxygen Consumption cc/gm/hr	Calories Per 24 Hours Per Mouse
Oct.....	25.5	2.86	8.2
Feb.....	34.9	2.55	10.6
April.....	31.0	2.83	10.2
Average.....	29.9	2.75	9.7

The FMR when applied to animals in the field should be considered a minimal figure of metabolism. Brody (1945: 477) considers that the maintenance energy expense is twice the basal metabolic rate. The energy cost of maintenance is the net dietary energy needed to carry on life processes, excluding the production of flesh, milk, or young.

To determine the caloric value of *Microtus* carcasses, four wild mice were sacrificed, minced, and dehydrated in a lyophilizing apparatus. This dried material was then burned in the bomb calorimeter to determine average caloric value per gm of dry mouse tissue. The wild mice were of average weight, rang-

ing from 10 to 39 gm, and did not exhibit large fat deposits around the internal organs.

Food consumption by mice was studied both in the field and in the laboratory. For the field studies, wild *Microtus* were snap-trapped every three months in other areas which were characterized by a bluegrass-perennial herb vegetation similar to that found on the study area. At least 24 mice were captured during each trapping period (Table 6). These mice were brought into the laboratory and their stomachs were removed and weighed. A portion of the stomach contents was placed on a glass slide with several drops of Turtex CMC-10 mounting media. A smear was made of this mixture and, after a cover glass was placed on the slide, the slide was examined under the low power objective of a microscope.

TABLE 6. Percentage importance of food materials from stomach samples.

Food Material	Fall	Winter	Spring	Summer
Number of stomachs	35	27	31	14
Grass.....	54	75	74	54
Herbs.....	28	18	23	44
Insects.....	T	T	1.8	T
Fruits.....	17	3	.1	1
Wood.....	1	4	.3	—
Seeds.....	T	—	.6	T
Moss.....	T	—	.1	T
Fungi.....	T	—	T	1
Grasses and herbs alone				
Grass.....	66	81	76	55
Herbs.....	34	19	24	45

A stomach content key was devised by feeding in the laboratory 5 *Microtus* on diets of natural foods, each mouse receiving only one food substance. These animals were sacrificed and slides of their stomach contents served as a reference key when examining the stomachs of wild mice. Under the microscope it was possible to distinguish the following food types: grasses, herbs, woody materials, roots, seeds, fruits, mosses, fungi, and insect remains. These identifications were made on the basis of cell shape, cell wall structure, arrangement of stomata, presence of parenchyma cells, sclereids, tracheids, and other elements. An estimate was made of the percentage that each food type contributed to the bulk of the plant material on each slide. The percentage importance of the food types was determined for the collection period by averaging the data for each individual stomach.

The quantity of food consumed was measured for caged mice in two laboratory experiments. In the first experiment, 15 mice in 5 cages were fed a "standard" laboratory diet of lettuce, carrots, and oatmeal (Whitnoyer 1956) for 30 days. In the second experiment, 5 mice were maintained on fresh-cut alfalfa for 30 days. Water was available in both experiments. Animals gained weight, bred, and gave birth to normal litters on both diets. Food materials

were weighed in and out of the cages daily; the weight loss of fresh food between weighings was determined by using a control cage. The information on food consumption is summarized in Table 7. The caloric value of the standard diet was determined from Wooster & Blanck (1950) and that of the alfalfa by combustion in the bomb calorimeter.

TABLE 7. Daily food consumption of individual mice on experimental diets.

	STANDARD DIET				Alfalfa Diet Alfalfa
	Lettuce	Carrot	Oatmeal	Total	
Consumption gms wet wgt. . .	24.8	10.2	4.4	39.4	28.1
Consumption gms dry wgt. . .	1.3	1.2	4.0	6.5	12.0
Caloric value of food per gm wet wgt.18	.45	3.96	—	—
Caloric value of food per gm dry wgt.	—	—	—	—	4.1
Calories consumed.	4.5	4.6	17.4	26.5	49.3
Ave wgt mice (gms)				46.0	46.0
Gms food consumed per gm mouse tissue.14	.26
Food Calories consumed per gm mouse tissue.58	1.07

The digestibility of the experimental diets was studied by collecting mouse feces in the cages for a 5-day period during each experiment. The feces were oven-dried and the caloric value determined in the bomb calorimeter. By this method it was possible to estimate the amount of gross energy in the feed which was undigested.

STUDIES OF THE LEAST WEASEL

The energetics of the least weasel were given a more superficial treatment than those of the vegetation, or of the *Microtus* population. Population estimates were inferred from the capture of weasels in live traps during the mouse trapping program and from counts of weasel tracks in the snow during December, January, and February. During any one trapping period, captured individuals were identified by weight under the assumption that only one individual of a particular weight would be present on the trap area. On the basis of trap records and tracking observations it appeared that there were two adult weasels on the area of 2.5 ha in the late fall of 1956. It was assumed that these weasels had been present and had produced young during the summer. The number of litters produced per year (two) and the number of young per litter (five) were accepted as reported by Burt (1948) and by Hall (1951). June and August were arbitrarily chosen as the birth dates of the litters.

Since no data on the growth of the least weasel were available, growth rates of adult and young weasels were estimated from the weights of captured animals. The initial weight for the adults in the early summer of 1956 was assumed to be 46 gm (average of 4 captures of young adults). These adults were assumed to have grown to an average adult weight of 60 gm by August (based on one cap-

ture) and to have maintained this weight through the spring of 1957. It was further assumed that the birth weight of the young was 3 gm and that each individual in the litter grew approximately 6 gm per month for the first 5 months and then 3 gm per month for the next 5 months. As with *Microtus*, production measurements were based on the instantaneous rate of growth of adults and young. Production was calculated separately for three 4-month periods (Table 8). Biomass measurements were converted to their caloric equivalent by using the factor obtained for mice carcasses.

Mortality was arbitrarily estimated as a loss of approximately 5 young, weighing 15 gm each, from September to December, 1956, and of one young, weighing 35 gm, from January to May, 1957.

Food consumption and digestibility of food were studied in the laboratory with one captured weasel (Table 9). In the course of two feeding experiments, one live mouse was placed in the weasel cage daily. The remains of the dead carcass of the mouse fed the previous day were transferred to a hardware-cloth envelope within the cage to indicate evaporation loss from the carcass. White mice (*Mus musculus*) were fed in the first study and laboratory-raised *Microtus* in the second study. Each experiment was run for a total of 30 days.

During the feeding experiment using *Microtus*, feces were collected for a 6-day period to measure food digestibility. The caloric value of these feces was determined in the bomb calorimeter.

The metabolic rate used for the least weasel was that obtained by Morrison (1957).

RESULTS

SOLAR ENERGY

The annual insolation per ha for 1956 and 1957 is shown in Table 10. Baten & Eichmeier (1951) indicate that the average agricultural growing season at East Lansing is from May 8 to October 4, with extremes ranging from April 8 to November 16. Field observations suggested that the growing season for natural vegetation of the old field was slightly longer than that for cultivated crops and extended from approximately April 1 (when spring plant growth became obvious) to approximately November 1 (when the accumulated production peak was reached in 1956). The total insolation during the 1956 growing season was 94.2×10^8 Cal per ha. Since approximately 50% of the incident energy (that in the ultraviolet and infrared portions of the spectrum) is not used by plants in photosynthesis (Terrien, Truffaut & Carles 1957, Daubenmire 1947), the total growing-season insolation was divided by two to give the usable insolation available to the plants. The data presented in Table 10 represent total solar insolation at the ground surface, and at the bottom of the table is shown the 50% correction of growing-season insolation. The corrected insolation value for 1956 is used in Fig. 1 and in all calculations of the ratio of insolation and production of the vegetation. The 50%

TABLE 8. Dynamics of least weasel population on one hectare.

Season	AVERAGE POPULATION NUMBER		TOTAL BIOMASS GRAMS		PROPORTIONATE WEIGHT CHANGE		PRODUCTION GRAMS		MORTALITY GRAMS		Respiration Loss Calories
	Adults	Young	Adults	Young	Adults	Young	Adults	Young	Adults	Young	
May-Aug.....	.80	2.0	42.4	10.3	1.30	2.58	11.1	10.0	0.0	0.0	1091
Aug.-Dec.....	.80	2.8	48.0	34.9	0.00	3.04	0.0	38.8	0.0	31.5	1884
Jan.-May.....	.80	1.6	48.0	61.9	0.00	1.76	0.0	35.5	0.0	10.5	2459

TABLE 9. Food consumption of the least weasel fed on live mice.

Species	FOOD CONSUMPTION		Caloric Value of Feces	Per Cent of Food Digested
	Grams	Calories		
<i>Microtus</i> ...	14.7	19.99	2.02	89.9
White mice..	15.1	29.50	—	—

reduction may be excessive during April, May and June when the total insolation at ground surface is reduced due to increased cloudiness. Clouds reduce the amount of ultraviolet and infrared radiation because of diffusion and absorption by water molecules (Terrien, Truffaut & Carles 1957) and it might be anticipated that under clouds more than 50% of the insolation at the ground would be usable by the plants.

TABLE 10. Solar insolation on the study area in calories per hectare per month for 1956 and 1957.

Month	1956	1957
January.....	4.2×10^8	5.0×10^8
February.....	7.3	6.1
March.....	9.5	11.0
April.....	10.8	9.9
May.....	14.7	13.9
June.....	17.8	16.8
July.....	15.3	18.2
August.....	13.6	15.2
September.....	12.2	11.7
October.....	9.8	7.9
November.....	4.5	3.9
December.....	2.7	3.8
Total.....	122.4	123.4
Total growing season (April 1 to Oct. 31).....	94.2	93.6
Growing season correction ¹	47.1	46.8

Data from the Michigan Hydrologic Research Station of the USDA and the Michigan Agricultural Experiment Station.
¹ 50 per cent of the total insolation during the growing season to allow for ultraviolet and infrared radiation which are not utilized in photosynthesis.

DYNAMICS OF THE VEGETATION

The production of the vegetation can be separated into two different components: (1) the production of the plant tops and the root biomass over the growing season, and (2) the photosynthate which is lost to consumption by animals and to respiration of the plant biomass. The production of tops and roots plus the material eaten by animals comprise the net production; the inclusion of the respiration yields the gross production of the vegetation. In measure-

ments of net production by the harvest method, consumption of green plant material by animals often is not included in the estimate of total net production. Here, food consumption by the mouse population is added to the production of the roots and tops, while food consumption by insects and other herbivores is not estimated or included.

The dry weight standing crop of vegetation (Fig. 2) shows a typical cycle of growth, death, and decay of vegetation. The grass-herb ratio shows cyclical fluctuations; grasses predominate in fall and winter, with a tendency toward equality in midsummer. A slight change in caloric content of the vegetation also occurred seasonally (Tables 11, 12). The peak above-ground standing crop was 385 gm per m² (3.85×10^6 gm per ha) in 1956 and 251 gm per m² (2.51×10^6 gm per ha) in 1957, these values being accepted as minimum estimates of production. The average caloric value of green vegetation was 4.08 Cal per gm dry weight (average of the values in Table 2).

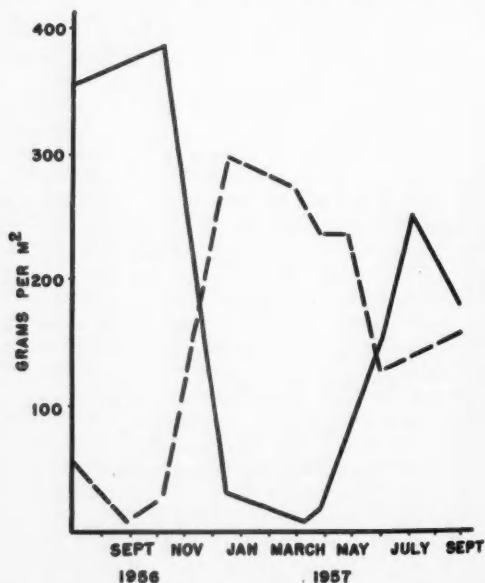


FIG. 2. The standing crops of living (solid line) and dead (broken line) vegetation by months in 1956 and 1957.

Standing crop of roots was measured three times during the 1957 growing season. The initial standing

TABLE 11. Above-ground standing crop of living and dead vegetation, and average caloric value of green grasses and herbs per square meter plot, and living grass-herb ratio.

Date Collected	Number of Plots	STANDING CROP LIVE		(GRAMS DRY WEIGHT) DEAD		Caloric Values Cal/gram Dry Weight	Grass:Herbs (Weight)
		Mean	SD	Mean	SD		
7/21/56.....	2	—	—	—	—	4.12	—
8/8/56.....	10	358.0	±49.2	55.6	±30.4	4.12	3.5:1
9/24/56.....	16	372.4	±81.2	8.0	—	4.30	9.1:1
11/2/56.....	20	385.2	±91.2	28.0	—	4.17	49.2:1
2/9/57.....	10	31.2	±12.8	300.0	±60.0	—	—
3/22/57.....	15	8.0	±2.4	274.0	±75.2	—	—
4/24/57.....	14	18.4	±6.8	234.8	±97.2	3.99	16.0:1
5/22/57.....	14	67.6	±12.8	236.0	±66.4	3.99	6.9:1
7/1/57.....	15	147.2	±49.6	126.8	±47.6	3.90	2.6:1
8/5/57.....	15	250.8	±71.2	140.4	±42.8	—	1.4:1
9/29/57.....	14	184.0	±71.2	164.0	±42.4	—	—

TABLE 12. The caloric value per gram of oven-dried plant tissue for various plant species collected during the study.

Date Collected	Species	Number of Samples	Cal/gm (Aver.)	S.D.
7/22/56	Poa compressa	5	4.12	±.08
8/8/56	Poa compressa	9	4.18	±.20
9/24/56	Poa compressa	14	4.31	±.45
11/2/56	Poa compressa	15	4.18	±.08
5/22/57	Poa compressa	3	4.02	±.05
7/1/57	Poa compressa	3	3.99	±.11
8/8/56	Linaria vulgaris	5	4.28	±.07
9/24/56	Linaria vulgaris	5	4.34	±.10
8/8/56	Daucus Carota	5	3.92	±.45
8/8/56	Cirsium arvense	6	3.93	±.22
8/8/56	Trifolium repens	2	4.09	±.20
8/8/56	Verbascum Thapsus	3	3.98	±.14
8/8/56	Plantago spp.	2	3.79	±.09
8/8/56	Dead grass	6	3.91	±.05
2/9/57	Dead grass	15	4.25	±.06
4/24/57	Grass and herbs	3	3.99	±.10
5/22/57	Herbs combined	3	3.97	±.12
7/1/57	Herbs combined	3	3.81	±.12
8/8/56	Roots	6	3.30	±.20

crop (1493 gm per m², 15 cm deep) was measured on April 13, 1957 when the vegetation was beginning spring growth. The second measurement was made on July 11, when the root standing crop was 1805 gm per m². The peak standing crop was 2516 gm per m² on September 29, 1957. The difference between the peak and initial standing crop approximated the organic matter synthesized and stored in the roots above 15 cm depth over the growing season (1023 gm per m²) in 1957. It was assumed that this rate was also applicable to the 1956 season. The caloric value of the roots, determined for a sample collected in August 1956 was 3.30 Cal per gm dry weight (Table 12).

The amount of live vegetation calculated to have been consumed by mice during the growing seasons in 1956 and 1957 is shown in Table 13.

Data on respiration of the vegetation were collected during four nights in the summer of 1957. The CO₂ released, O₂ consumed, RQ, and Cal used per

TABLE 13. Food consumption of *Microtus* populations during the 1956 and 1957 growing seasons.

Date	Interval Days	Density Mice Per Hectare	Individual Mean Weight Grams	Population Biomass Grams	Consumption Grams Per Hectare
1956					
April 1.....	52	5.0	29	145	1,056
May 22.....	63	5.2	29	151	1,329
July 24.....	42	9.6	29	278	1,634
Sept. 4.....	35	16.5	29	479	2,349
Oct. 9.....	22	21.2	31	657	2,024
Total.....					8,392
1957					
April 1.....	53	64.2 ¹	32	2054	15,243
May 23.....	26	49.8	26	1295	4,714
June 18.....	36	65.4	28	1831	9,227
July 24.....	61	61.4	30	1842	15,732
Sept. 23.....	38	111.2	26	2891	15,379
Total.....					60,295

¹ Average of March and April population estimates.

gm of plant per night are shown in Table 14. The product of the rate of respiration in Cal, the mean standing crop of vegetation and the number of days between measurements of respiration yielded the Cal used in night respiration by the vegetation over the growing season, 146.2 Cal per m² plot or 1.46 × 10⁶ Cal per ha (Table 15).

TABLE 14. Night respiration of old field vegetation.

Date	CO ₂ Produced cc./night	O ₂ Consumed cc./night	RQ	Calories per cc. Oxygen	Grams Vegetation ¹	Calories per Gram per Night
5/17/57	1.96	3.50	.56	.0045	.398	.041
5/25/57	1.36	1.91	.72	.0047	.589	.016
6/13/57	1.17	1.20	.97	.0050	.866	.007
7/20/57	.90	.68	1.31	.0053	1.905	.002

¹ Grams of vegetation on area covered by cans (86.6 cm²) derived from the graph of standing crop of vegetation (Fig. 1).

Thomas & Hill (1949) in their field studies on the respiration of alfalfa showed that night respiration of the tops was approximately one-half the day respiration and that the root respiration was about equal to the combined day and night top respiration.

TABLE 15. Night respiration of the vegetation biomass during growing season.

Date	Interval Days	Mean Standing Crop Vegetation Grams	Respiration Rate Cal/gm/night	Respiration Loss/m ² Cal.
April 1 to May 21.....	51	6.1	.041	50.4
May 22 to June 2.....	12	16.7	.016	12.4
June 3 to July 2.....	30	27.6	.007	23.2
July 3 to Nov. 1.....	121	62.2	.002	60.2
Total.....				146.2

If we assume that these findings can be applied to the old-field vegetation, the day respiration of the tops would equal 2.92×10^6 Cal per ha, and respiration of the roots, 4.38×10^6 Cal per ha. Total respiration of the entire plant biomass would be approximately 8.76×10^6 Cal per ha or 15% of the total assimilation. This estimate is slightly less than those of Transeau (1926) and Thomas & Hill (1949). These workers suggest that respiration of the plant biomass amounts to 25-35% of the total production. It is not known if the discrepancy between estimates made in this study and those by Transeau and Thomas & Hill is due to a diffusion of gases between the soil and air under the cans, or if it represents a real difference between the respiration of natural vegetation and cultivated crop plants.

In 1956 and 1957 the production was made up of the following components:

	1956	1957
Production of tops	3.85×10^6 gm/ha	2.51×10^6 gm/ha
Root production	$10.23 \times$ "	$10.23 \times$ "
Consumed by <i>Microtus</i>	$.01 \times$ "	$.06 \times$ "
Weight net production	$14.09 \times$ "	$12.80 \times$ "
Calorie net production	49.51×10^6 Cal/ha	44.25×10^6 Cal/ha
Respiration	$8.76 \times$ "	$8.76 \times$ "
Calorie gross production	$58.27 \times$ "	$53.01 \times$ "

THE DYNAMICS OF THE *Microtus* POPULATION

The energy dynamics of the *Microtus* population were separated into several components: (1) the tissue production, (2) energy expense of respiration, and (3) the intake of energy through foods. The estimate of tissue production was, in turn, based on determinations of the standing crop of mice, production of young, and rate of growth of mice in all age categories. To relate *Microtus* to the vegetation base of the food chain, determinations of consumption and digestibility of foods were used to estimate the percentage of the available food consumed by the mice, and the percentage of the consumed food used in metabolic processes and stored as tissue production. Finally, each separate component was brought together in Fig. 1 to show the entire exchange through the *Microtus* population.

Standing Crop of *Microtus*

The standing crop of *Microtus* showed some unexpected variations during the investigation (Table 1). The population at the beginning of the study was at

a very low level (5.2 mice per hectare). In fact, following the first trapping program in May 1956, an attempt was made to relocate the study on another area with a higher population of *Microtus*. It was not known whether this "low" was the result of adverse weather, heavy predation, or "cyclical behavior."

The estimated peak population (139 mice per hectare) determined in this study could not be considered unusual for the species. Other workers have arrived at greater estimates of population density for *Microtus pennsylvanicus*, 291 per hectare (Bole, 1939), 395-567 per hectare (Hamilton, 1937), and 165 per hectare (Townsend, 1935). The months in which the peak density occurred was unusual. Hamilton (1937), Martin (1956) and others showed that *Microtus* generally reach a peak population in the fall (September to November) after which the population decreases until breeding begins again in the spring. Linduska (1950), on the contrary, found that the annual peak population at Rose Lake, Michigan, approximately seven miles north of this study, occurred in January and February, as in the present study. Linduska was unable to explain the difference between his results and those of Hamilton, but suggested that the winter peak may be a local adaptation to "xerophytic" conditions.

A more detailed knowledge of the population density and topography of the study area enabled the writer to suggest another explanation for the

winter population high. A region of dense cover, composed primarily of bluegrass sod, occurred in the center of the trap area. This dense cover may have served as a place of refuge for the mice during alternately wet and freezing weather occurring in January, February, and March. The number of new captures per day of trapping was correlated with snowfall (Table 16) suggesting that snow storms stimulated increased movement of the mice. Since in November and January the increased captures of new animals occurred late in the trapping period, it was thought that these captures represented new animals moving into the trap area rather than movement of the resident population. The movements immediately before and during snowfall were considered to be due to a migration of mice from upland areas into the areas with heavier cover, resulting in an increased population on the study area during the storm periods and possibly throughout the winter.

The fraction of animals captured in common to both lines decreased in January, February, and March (Table 1). This seasonal variation may have been

TABLE 16. Snowfall and new captures of *Microtus* in three winter months compared with a typical summer month.

Day of Trapping	NOVEMBER		JANUARY		FEBRUARY		JULY	
	Snow ¹	Captures	Snow	Captures	Snow	Captures	Snow	Captures
1.....	.00	2	.00	1	.00	3	.00	4
2.....	.00	3	.05	1	.00	4	.00	11
3.....	.00	4	.01	2	.10	10	.00	4
4.....	.00	3	.28	8	.00	9	.00	6
5.....	.10	8	.17	2	.00	3	.00	9
6.....	.50	2	.01	1	.00	7	.00	3
7.....	T	0	T	2	T	1	.00	2
8.....			.85	11				
9.....			.05	0				

¹ Snowfall or sleet in inches, taken from U. S. Department of Commerce, Local Climatological Data for East Lansing, Michigan.

the result of decreased size of the home range of the mice and consequent shorter daily movements. These in turn, may have resulted from increased density of mice or from some characteristic of winter weather acting on mouse behavior. Further information is needed before the cause for the decrease in number of captures in common in the winter can be established.

The observed fraction of animals captured in common to both lines for January (4.5%) was lower than that fraction used in Table 1. The January trapping period was interrupted by heavy snowfall and it was possible to run the trap lines only 3 days in one period and 4 days in another. If the unusually low fraction .045 is used to determine population density a very high population estimate (256 per ha) results. It was thought that this high a density was unlikely, since it would require a six-fold increase in the population in two months. Therefore, the fractions of common captures for the other winter months (February and March) were averaged and this average was used to estimate the January population.

Caloric Value of *Microtus* Tissue

Since the objective of this study was to determine the energy transfer and losses between the levels of the food chain, it was necessary to convert the production data, calculated initially in terms of weight, into Calories (Table 17). In the process of preparing mice for calorific analysis, the mice lost approximately 71% of their body weight. Since mouse production figures were computed in terms of live weight, the average caloric value per gm of mouse tissue had to be converted from dry weight (4.65 Cal per gm) to live weight (1.37 Cal per gm).

Mortality or Emigration of the Mice

Mortality and emigration both result in the disappearance of mice and are considered collectively in this report. When an animal was not caught again, it was impossible to determine whether it had died or had moved out of the trapping area. In a few instances animals were trapped in one month and not retrapped until several months later. Where these

TABLE 17. The wet weight, dry weight, and the average caloric value per gram dry *Microtus* tissue determined for four male mice (standard deviation in parenthesis).

Individual	Age	Live Weight	Dry Weight	Caloric Value of Tissue
1.....	adult	39.1	11.9	4.49 (± .21)
2.....	adult	24.5	7.0	4.67 (± .25)
3.....	adult	28.0	8.1	4.63 (± .26)
4.....	juvenile	10.0	2.9	4.82 (± .07)
average (pooled data).....				4.65 (± .21)

animals resided in the intervening period is unknown, but it is here assumed that they were on the trap area.

The mortality of juveniles and adults was greatest immediately after the peak population was reached in February (Table 1). This peak was possibly correlated with periodic inundation of the low portions of the study area in February and March. As was mentioned previously this population decrease was expected to occur in December but may have been postponed by an immigration of mice into the trap area in January and February. Because of the fire on the study area in March, a measure of the mortality rate was unavailable for February. Mortality was assumed to be 55% in this month (based on the difference between the population estimates for February and March on the two adjacent areas).

Production of Young by Adults

The potential number of young produced by the population showed a consistent increase from 24.8 mice per ha in May to 137.9 mice per ha in November 1956, and from 15.2 mice per ha in March to 79.3 mice per ha in April 1957 (Table 3). During January and February no females were judged to be in breeding condition and it was assumed that no breeding occurred. This assumption is consistent with the findings of Hamilton (1937). During the first four months of the study data on the breeding condition of the females were not collected. The pregnancy rate for these periods was later assumed to be approximately 90%.

TABLE 18. Population dynamics of nestling young on one hectare.

Date	Potential Production Numbers	Replacements ¹ Numbers	Survival Rate Per Cent	Mean Biomass of Young Grams	MORTALITY		Immigration Numbers
					Grams	Calories	
May.....	24.8	14.5	58	144	78	107	—
July.....	28.5	12.7	45	135	108	148	—
Sept.....	34.8	18.3	53	180	114	156	—
Oct.....	64.5	38.0	59	333	176	241	—
Nov.....	137.9	63.8	46	893	693	949	—
Jan.....	0.0	0.0	—	—	—	—	96.0
Feb.....	0.0	0.0	—	—	—	—	—
March.....	15.2	27.4	100	100	0	0	13.4
April.....	79.3	44.1	56	361	209	286	—

¹ Number of young replacing adults disappearing through death or migration.

The potential natality suggests the maximum possible number of young which could be produced by the population, and may be the source of most of the population increase and of replacements for adults disappearing from the population. The number of young entering the trap-susceptible population was assumed to be equal to the number of adults and juveniles disappearing between trapping periods. These replacement young also showed a consistent increase from spring to fall (Table 18) and in all but March were fewer in number than the potential production of young.

Production of Tissue

Production of tissue in the mouse population was calculated for each trapping period from a knowledge of the average population biomass and the observed rates of growth. This calculation was carried out separately for the various weight classes, the production of tissue being estimated by methods described earlier. For each class the average biomass between times of trapping was estimated as the mean value of the corresponding population biomass determinations made at each trapping. The rates of growth were determined from weights of individual mice recaptured in two consecutive trapping periods.

On occasion certain weight classes, while obviously contributing to the population biomass, were not represented by recaptured animals, and hence, no growth rates were available for these classes. In Table 2 these instances are distinguished. Since it was known that some of the classes not represented by recaptured mice contributed to the production of tissue, it was necessary to estimate appropriate rates of growth for weight classes known to be producing tissue.

To estimate missing growth rates, use was made of the fact that growth rates decreased progressively with increasing weight, in each time period. This fact is obvious in Table 2 where the proportional weight changes, unadjusted for length of interval, show that over the year the average weight change for mice in the 11-20 gm class exceeded the average change for the 21-30 gm class by a factor of 0.66. Similarly, the 21-30 gm mice exceeded the 31-40 gm animals by 0.30. For those classes for which information was lacking on growth rates, as detailed above,

substitute values were approximated by adding the above average increment in proportionate growth to the observed proportionate change for the next heaviest weight class. For example, in October 1956, 0.66 was added to the value of 1.20 observed for the 21-30 gm mice to estimate the missing value for the 11-20 gm animals.

In every instance survivors in the 41-50 gm class lost weight (Table 2). Hamilton (1941) suggests that the heavier adult mice lose weight only in the winter, but these data indicate that weight loss is characteristic of the 41-50 gm weight class throughout the year. This weight loss does not appear to be correlated with senility because in no instance did a heavy animal showing a weight loss disappear in the trapping period immediately following the loss in weight. Over the winter months of January and February mice in most other weight classes also lost weight. These losses probably represent the exhaustion of body fat stored over the fall months.

The weight distribution graph (Fig. 3) reflected the internal dynamics of the mouse population. Since weight may be considered a rough criterion of age, it would be expected that the greatest number of mice would fall in the lightest weight classes. However, no mice were caught in the 1-10 gm weight class, except in May. Whitmoyer (1956) found in his study of the growth rate of laboratory-raised *Microtus pennsylvanicus* that the eyes of all young were open at 11 days of age, at an average weight of 9 gm. Hamilton (1941) also showed that young *M. pennsylvanicus* did not leave the nest until they were 10 gm in weight, at 9-13 days of age. Therefore, it was assumed that nestling young did not leave the nest before they attained a weight of 10 gm, and that the probability of capturing an animal weighing less than 10 gm was very small.

Blair (1948) states that small meadow mice old enough to leave the nest may be caught by live traps. If the probability of capture were the same for all weight classes, in those months in which reproduction occurred we would expect the highest number of captures to be in the 11-20 gm class. However the 11-20 gm class in each month except one (May) had fewer mice than did the 21-30 gm class (Fig. 3). The home range of very young mice may be smaller than

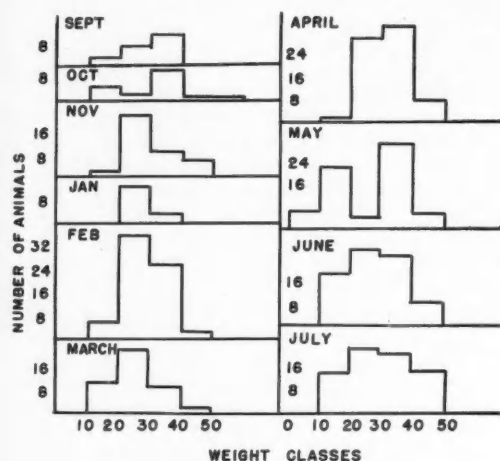


FIG. 3. The number of animals per weight class captured during each trapping period.

that of adults, resulting in a lower probability of capture of juvenile mice and a proportionately lower representation of this class of mice in the data. A second explanation for fewer animals in the 11-20 gm class than expected may be that the rapid growth of these mice shortens the period of exposure to trapping for individuals in this weight class. Hamilton (1941), observing the lower proportion of light-weight mice in his trapping data, suggested that exceptionally heavy mortality in this weight class may be further cause for the phenomenon. Whatever the cause, if the probability of capture for the 11-20 gm mice is less than for the 21 gm and heavier animals, the determination of the biomass of the population based on live-trapping data might underestimate the contribution of the 11-20 gm weight class.

The growth rates of nestling young (Table 4) were generally quite similar over the year since the growth rates were calculated from a constant birth weight of 3 gm and the relatively constant weight of the lightest juvenile captured in the traps. Since the nestling young had the highest growth rates, they contributed a larger share of the tissue growth or production over the period of study (Table 4) than did the adults and juveniles (Table 2).

Immigration into the Study Area

In January and March the potential production was insufficient to account for the increase in the population and/or the mortality of adults and juveniles. To account for the discrepancy between the potential production and the number of young entering the trap-susceptible population, it was assumed that mice migrated into the study area. In March this type of immigration was of a relatively minor nature, amounting to only 21% of the mean adult population. In January, however, the immigration was of greater importance since the population almost doubled between January and February (Table

1). There were no young produced in January; therefore, all of this increase must have been due to immigration. This assumption is supported by the previous information of the winter movements of mice immediately before or during snow storms (Table 16), which were interpreted to mean a migration of mice into the study area.

Theoretically, since the population increased in size over the period of study, the energy lost to mortality should not exceed that appearing in tissue production. However, Table 19 shows that mortality exceeded production in every period studied. Since the standing crop increased over the year by 1569 Cal (Table 1), production plus immigration must have exceeded mortality plus emigration by this amount. These last two processes exceeded production alone by approximately 12,000 Cal (Table 19).

TABLE 19. Tissue production, mortality, and respiration of mouse population in calories per hectare.

Period	PRODUCTION		MORTALITY		RESPIRATION	
	Entire Period	Per Day	Entire Period	Per Day	Entire Period	Per Day
May to July.....	331	5	500	8	4,871	76
July to Sept.....	309	8	380	9	5,607	119
Sept. to Oct.....	488	14	605	20	6,808	195
Oct. to Nov.....	787	20	951	24	10,578	271
Nov. to Jan.....	1732	29	2,111	35	33,245	575
Jan. to Feb.....	—	—	1,245	36	27,655	773
Feb. to March.....	—	—	3,284	122	37,514	1391
March to April.....	727	20	957	26	27,710	770
April to May.....	786	28	2,217	79	17,059	609
Total.....	5170		17,200		169,877	

The conclusion follows that immigration (termed import in Fig. 1) must have contributed approximately 13,500 Cal. The estimates of immigration in Table 18 account only for the difference in calculated production of young and the young needed to replace trap-susceptible adults and juveniles. These estimates are included in the above calculations.

Energy leaving one population of mice by emigration joins another by immigration. Over all populations, these gains and losses must balance, just as production of all populations must equal the sum of mortality and population change. In this particular instance, immigration appears to have involved over twice as much energy transfer as production within the population itself. It is not known whether this population, sustaining a heavy population pressure as calculated from the weasels alone, represents a "sink" with energy flowing only inward, or whether it may approach an energy equilibrium, with the weasel and other predators being in equilibrium with the local production and there being a sizable exportation of energy from the population.

Immigration adds energy to a population, increasing the biomass, but not by any process defined here as production. Production of these animals took place elsewhere, and hence, cannot be credited to the local population. On the other hand, energy losses

from the respiration of immigrants may have considerable influence on the energy balance in the community. Inspection of Table 1 and 19 will show that immigration increased the biomass greatly during January and February, accounting for a large part of the high population metabolism or respiration.

Respiration of the Mouse Population

An estimate of the minimum number of Calories used by the mouse population in respiration was obtained from the fasting metabolic rate of *Microtus*. These rates showed very little variation seasonally (Table 5). Although an analysis of variance in the metabolic rates of individual groups in each calorimeter jar showed that no significant differences in the rates between seasons or within experiments, seasonal variations are to be expected. These were probably obscured by confining the mice in the laboratory at a constant temperature while measurements were being made. The average metabolic rate of 10 Cal per 24 hrs per mouse was used as the minimum metabolic constant to determine the minimum respiration of the mouse biomass (Table 20).

TABLE 20. Respiration of the mouse population.

Date	Respiration of Young Calories per Hectare	Respiration of Adults Calories per Hectare
May.....	1,575	3,296
July.....	975	4,032
Sept.....	1,050	5,758
Oct.....	2,329	8,249
Nov.....	7,381	25,864
Jan.....	—	27,055
Feb.....	—	37,544
March.....	620	27,090
April.....	2,177	14,882
Total.....	16,107	153,770

The average metabolic rate determined in the present study, 2.75 cc O₂ per gm per hr, compares favorably with the determinations on *Microtus pennsylvanicus* made by Pearson (1947), 1.9–2.8 cc/gm/hr, and Morrison (1948), 1.8–2.8 cc/gm/hr. Hatfield (1939) studied metabolism in *Microtus californicus* but arrived at a much higher figure of metabolism, 5.2 cc/gm/hr. Pearson suggested that the higher metabolic rates obtained by Hatfield were due to greater activity during the periods of measurements.

The metabolic rate determined by this study was a minimal rate and when used in calculations of energy loss by respiration underestimated the actual loss. The average metabolic rate of *Microtus* in the wild is unknown. Morrison (1948) gives some indication of what this average rate would be; in his studies, the average metabolic rate of *Microtus* held in the calorimeter for 24 hrs, with food and water provided, was 18–42% above the minimum rate of metabolism.

Summary of *Microtus* Energy Assimilation

The summary of the energy assimilation of the *Microtus* population (Table 19) shows the assimilation of a population changing from a low density to a higher density. With the exception of January and February, when growth of young and adult mice did not occur, tissue production rose continuously during the spring, summer, and fall of 1956, and the spring of 1957. Mortality, including the disappearance of mice from the population by death, predation, or emigration, also showed a smooth rise, with a disproportionate increase in February. Respiration was proportional to the population biomass and increased until the population drop in March. Following this, the energy loss due to respiration began a second increase. Laboratory metabolic measurements allowed no estimate to be made of expected seasonal changes in the respiration energy cost.

The respiration loss, though a minimal estimate, accounted for by far the greatest amount of energy used by the *Microtus* population. Respiration accounted for 68% of the energy passing through the mouse population yearly. In comparison, the mean biomass of mice (1900 Cal per ha) represented a storage at any one time of only 1.0% of the annual energy consumption; the maximum biomass (Table 1) was only 3% and the minimum biomass 0.1% of the annual energy consumption.

Digestibility of Food

The amount of food ingested and its energy value may be understood in relation to the metabolism of the mouse population only through some knowledge of the digestive processes and their efficiency. The gross energy in the food minus the energy in the feces equals the digestible energy (Brody 1945). The feces include secretions and cells sloughing into the digestive tract. Thus the digestible energy indicates only the excess of food energy taken into the blood stream over excretion into the gut.

The digestibility of the food was investigated briefly in the laboratory, with results from three animals as indicated in Table 21. Although requiring confirmation, they indicate an exceptionally high digestibility for alfalfa in *Microtus* (90% of the gross energy as against the figure of 50% given by Morrison 1949 for cattle and sheep.) Further, with the diet of lettuce, carrots, and oatmeal, 82% of the gross energy was digested, equalling the presumed digestive efficiency of humans with the same diet, as calculated from the tables of Merrill & Watt (1955).

Further work in this direction is needed to understand the trophic ecology of *Microtus*, as well as other small mammals. Attempts should be made to determine the digestibility for various single dietary components and for complete diets. The qualitative composition of the diet also requires investigation, as suggested in the following section.

Consumption of Food

The amount of food consumed, considered with digestibility, constitutes the trophic levy upon the

TABLE 21. Digestibility of laboratory diets.

Day	Caloric Intake in Food	Caloric Loss in Feces	Undigested (per cent)
Alfalfa diet—2 female <i>Microtus</i>			
1.....	128.7	20.2	15.7
2.....	183.1	15.2	8.3
3.....	83.3	12.9	15.5
4.....	143.5	12.0	9.0
5.....	176.1	12.4	7.0
average (pooled data).....			10.2 (± 4.2) ¹
Standard diet—1 male <i>Microtus</i>			
1.....	26.1	4.3	16.5
2.....	21.3	4.3	20.2
3.....	28.9	4.4	15.2
4.....	21.5	4.3	20.0
5.....	23.3	4.2	18.0
average (pooled data).....			17.8 (± 2.2)

¹ Standard deviation in parenthesis.

environment by the population. Food consumption may be estimated in several ways; here it has been done by laboratory means (Table 7) and by examination of the stomach contents of wild mice (Table 22).

TABLE 22. Weight of stomach contents of snap-trapped mice.

Season	Number Weighed	Mean Wgt Mice Grams	Mean Weight of Contents Grams	Standard Deviation Grams	Calculated ¹ Daily Food Consumption Grams
Fall.....	28	28	1.15	$\pm .83$	23.0
Winter.....	27	28	1.35	$\pm .68$	27.0
Spring.....	21	35	1.17	$\pm .59$	23.4
Summer.....	24	27	1.31	$\pm .68$	26.2
average.....					24.9

¹ Under the assumption that the mean weight of stomach contents represents one-half the stomach capacity and that the mice have 10 feeding periods per day.

Food consumption of *Microtus* has long been of interest to investigators, partly for economic reasons. Bailey (1924) fed *Microtus* a diet of clover, cantaloupe, grain, and seeds and found that they consumed 55% of their body weight daily. Regnier & Pussard (1926) obtained similar results with *Microtus arvalis* on a mixed diet of oat seeds, oat stems, and mangolds. In an experiment on which *Microtus* were fed a diet of dry feed (rolled oats, dry skim milk, dry meat, and seeds), Hatfield (1935) found an average consumption of 3.48 gm of food per mouse per day.

In the present study the mice on the standard diet consumed more fresh food than did the mice on the alfalfa diet. When dry weight of the food and caloric value was considered the reverse was true. It appears from these results and with comparison with Hatfield's findings that inclusion of dry foods in the diet re-

duced food consumption on a weight basis. The dry food materials (oatmeal, seed, etc.) have a much higher caloric value than fresh leafy foods such as lettuce and alfalfa, and animals on a fresh diet of succulent foods might have to consume a greater quantity of food to satisfy their energy requirements. In the present study, the mice on the alfalfa diet consumed 61% of their body weight daily and those on the "standard" diet consumed 86%. In both instances, the food consumption as a percentage of body weight was greater than that found by Bailey (1924) and Regnier & Pussard (1926).

Since blue grass appeared to be the dominant food plant of the environment in the study, attempts were made to maintain *Microtus* on a diet of fresh-cut, mature blue grass, with water available. In two attempts most of the animals lost considerable weight, or died, as indicated below:

Trial	Number Mice	Number Dying	Number Losing Weight	Number Gaining Weight
1	6	2	2	2
2	4	2	2	0

Dice (1922) was able to maintain *Microtus ochrogaster* on blue grass; possibly he fed immature grass or grass sod which might have a higher nutritive value. The energy content of the blue grass was 4.13 Cal per gm dry weight, which was closely similar to the caloric value of alfalfa (4.12 Cal per gm); however, the protein content of mature blue grass (6.6%, Morrison 1949) is much lower than that of alfalfa (14.8%, Morrison 1949). Lack of protein may be a cause of my failure to maintain *Microtus* on a blue grass diet. Regnier & Pussard (1926) found *Microtus arvalis* ate meat readily, consuming other voles and insects (Carabidae). They suggest that this consumption of protein might influence the numbers of mice during plague years. During one experiment in the present study, one *Microtus* ate 15 large grasshoppers within 24 hours. *Microtus* may thus supplement a low protein diet with insects or other high protein foods.

The stomach contents of animals taken by snap-traps reveal the proportional composition of the diet, assuming all components to be digested at the same rate (Table 6). To infer food consumption from the information on the volume of food in stomachs further, information on the rate of stomach clearance through digestion is required. Such information is not available, but one may infer from the observations of Hatfield (1940), Davis (1933), and Pearson (1947) that wild mice characteristically have 8-12 activity periods during a 24-hr day, and that these periods are concerned with feeding activity, to fill a nearly empty stomach.

The quantitative information on stomach contents (Table 22) may be examined, under the assumption of 10 activity periods a day, and a filling of the stomach to twice the mean observed contents at each activity period. The assumption that the mean stomach content equalled half a full stomach is supported not only

by theoretical sampling considerations, but also by the observation that the observed stomachs ranged from full to almost empty, with most being "half-full."

The overall estimate of about 25 gm of food eaten per day (.86 gm wet food per gm mouse), for all sizes of capture-susceptible mice, agrees fairly well with the laboratory-determined values of 39 and 28 gm (.86 and .61 gm wet food per gm mouse) for two different diets. It is not known whether the indicated seasonal fluctuations are real or reflect bias from either shifting activity patterns, changing age structure, or sampling variation. However, this method of observation seems to offer a practical, if approximate, method of measuring food consumption.

The differential seasonal consumption of available food materials in Table 6 showed that grass (grass and sedges) was the dominant food at all seasons. Dead vegetation (with the exception of wood) was not found in the stomach slides, therefore, it was assumed that dead vegetation was not used by *Microtus*. Since the clip quadrat used to determine food availability and production of vegetation only sampled grasses and herbs and not mosses, fruit, and other foods, the separate percentages of grass and herbs in the stomachs were also calculated (Table 6).

The food consumption of the population was estimated by multiplying the biomass of the trap-susceptible population by the food consumption (.14 gm dry food per gm of mouse tissue per day or .58 Cal per gm of mouse tissue per day) of captive mice on the standard diet. Food consumption determined with the standard diet was used because it was thought that the standard diet more closely represented the diet of wild mice. Total consumption of vegetation per trap period by the mouse population was 250×103 Cal.

THE LEAST WEASEL POPULATION

During the study least weasels were captured in 15 live-traps and were tracked on three different days during the winter. The largest number of individuals captured in one trap period was 4 (May 1957). Examination of the entire area on three days in winter (in each instance the morning following a snowfall of the previous day) yielded the tracks of one weasel in December, two in January, and three in February. According to Polderboer (1942) the maximum home range of the least weasel is 2 acres. Since the study area averaged 6.2 acres in size, it was assumed that at least three or four adult weasels could live on the area. Although the first evidence of weasels was not noted until July, 1956, it was assumed that two weasels were present at the beginning of the study in May, 1956.

Burt (1948) states that two litters of young are born per year. Litter size ranges from 4 to 10 (Burt 1948) and averages 5 (Hall 1951). If 2 litters of 5 young were produced by the weasels over the year, it is estimated that approximately 12 weasels were present on the area in September, 1956. This population of 12 animals decreased to 6 animals in May 1957.

The mean weight of the young dying in the period August to December was estimated at 15 gm, and in January to May at 35 gm. Although the population values may appear unusually high since the least weasel has been considered a rarity in Michigan (Hatt 1940), the evidence available supports these estimates.

Under the assumption that the population of least weasels followed the model developed in the section on methods and further elaborated in the above introductory paragraphs, the production of tissue by the weasels remained rather steady throughout the year (Table 8). In the summer, production of tissue was due to growth of both adults and young. In the fall and winter, the population of young, decreasing from 10 to approximately 5 animals, contributed all of the growth in this period. In the late winter and spring, the population of young, decreasing from 5 to 4 animals, again furnished all of the growth of tissue.

The respiration energy loss of the weasel population, based on an average minimum rate of O_2 consumption of 1.61 cc per gm per hr (Morrison 1957), increased over the year of study (Table 8). As observed with *Microtus*, the energy used in respiration of the weasel biomass was considerably greater than that involved in tissue production.

The laboratory feeding experiments were used to evaluate the role of the least weasel as a predator on *Microtus*. *Microtus* were assumed to be the sole food used by the weasel (Hatt 1940). In the laboratory experiments, the captive weasel consumed either 15.1 gm of white mice or 14.7 gm of *Microtus* per day (Table 9). Llewellyn (1942) found a similar rate of consumption in studies with a 32-gm weasel, i.e. 19.7 gm of mice per day. An average food consumption of 15 gm of mouse tissue per day was assumed to represent the true food consumption of adult weasels over the year. The young weasels, like other mammals (Morrison 1949), would probably use less food per day than the adults, and the daily food consumption of young was estimated to be 5 gm per day from May to August and 8 gm per day from August to December. Using these constants as a basis for calculating true food consumption, the effect of the weasel on the *Microtus* population was estimated. The weasel population consumed 5,824 Cal annually; this consumption was 3.07 times the mean biomass of *Microtus* (1900 Cal) over the year. Since net production of the *Microtus* population totaled only 5,170 Cal per ha annually, the weasel population appears to have required energy in excess of that produced by its principal prey. As previously noted, the production of the *Microtus* population did not allow for the energy imported by the mice which moved into the area. Further, it is possible that the weasel had other sources of food, such as *Blarina* which existed in moderately large numbers on the area, and insects, which were abundant during the summer, or perhaps the calculations of weasel population density here are in error.

The percentage of the energy in the mouse car-

casses which was digested by the least weasel was determined in the digestibility experiments. When the weasel was on the *Microtus* diet, he was able to digest 89.9% of the energy in the mouse bodies (Table 9). This rather high efficiency of digestion is comparable with the somewhat lower efficiency of digestion (70-80% of a dry-feed diet, McCay 1949) for the dog.

DISCUSSION

In the transition of energy between two steps of the food chain there are two main pathways by which energy can be lost or diverted from the food chain itself. First, in tracing the energy from one population to the next not all the food organisms will be consumed by the consumer species; some of this energy could be dispersed to another food chain by migration of the food species out of the study area, by consumption of the food species by organisms outside of the food chain, or by death. These are considered to be energy losses of the first order. Second, not all the energy consumed is used in growth or in production of young; some of it is diverted to the maintenance of the organism and some passes through the body unused. These are energy losses of the second order. In energy losses of the first order the energy lost from the food chain is still in a form available for use by other animals. In energy losses of the second order, the loss is primarily heat derived from metabolic processes which is unavailable for further use by the food chain; that passing through the body is, of course, available to various other organisms in the food web.

ENERGY LOSSES OF THE FIRST ORDER

Of the solar energy available to the vegetation over the growing season (one-half of the total incident insolation during the growing season), 1.2% was utilized in the gross production, and 1.1% in the net production of the vegetation (Fig. 1). These figures can be compared with the giant ragweed ecosystem in Oklahoma, 1.2%, and alfalfa growing in experimental plots for 6 months, 3.1% (data converted from tabular material in Odum, 1959—net production was divided by incident energy data for Michigan). Data on the percentage of solar energy utilized by the vegetation of different communities are still too limited to allow any comparison of the efficiencies of a successional community with a stable one. At this time we may say only that terrestrial vegetation of the old field community on this soil, at this site, and for these years appeared to utilize approximately 1% of the available solar energy during the growing season.

The net production of the vegetation can be considered as the energy available to the herbivorous animals in the community. *Microtus* is primarily a herbivore, with animal food appearing only in trace amounts over the year (see Table 6). It was assumed in this study that only the production attributed to the above-ground vegetation could be utilized by *Microtus*. Some of the root biomass was undoubtedly

also used by the mice, but no estimate of the extent of root utilization was available. Lantz (1907) and Bailey (1924) state that consumption of roots is relatively unimportant, except during the winter, and roots were not recorded among the stomach contents in the present study. It is assumed here that use of roots was negligible.

Of the energy in the vegetation presumably available to the mice (15.8×10^6 Cal), 1.6% was consumed, with 1.1% utilized by the mice in production and respiration. These percentages assume no loss of vegetation due to cutting of stems and leaves by *Microtus*. The utilization of the energy in the vegetation not consumed by mice was not traced further in this study. Some of this energy was probably diverted through invertebrate food chains. Wolcott (1937) indicated that insects ate $.94 \times 10^6$ gm (3.76×10^6 Cal) of above-ground vegetation per ha in a pasture in New York over the summer. This level of consumption would amount to 23.9% of the available energy in the old field vegetation of the present study. If these data are correct, insects may be considered as more important herbivores in this old field community than are the meadow mice.

As mentioned previously, the energy in the *Microtus* population (production) available to predators was augmented by an import of energy through immigration of mice into the study area. This immigration was particularly noticeable in the winter and spring of 1957. Of the total energy available in the *Microtus* population (production plus immigration, Fig. 1) the least weasel consumed 31% as food and used 30% in production and respiration; considering only the production of the mice, the weasel consumed over 100%. When the energy consumed by the weasel and the energy retained in the mouse population through an increase in population size from May 1956 to May 1957 was subtracted from the production plus energy imported through immigration, 43% of the energy of the mouse population was unaccounted for. This loss may be attributed to emigration, to death from disease or accident, and degradation through micro-organism food chains, or to capture in other predator chains. Some possible predators are *Blarina brevicauda* (Eadie 1952), *Felis domesticus* (Toner 1956, Korschgen 1957), or Owls, Red-tailed hawks, Red-shouldered hawks, and Cooper's hawks (Linduska 1950). All of these predators were seen on the study area during the investigation.

Most of the calculated production of the weasel population could be accounted for by the increase in the size of the population from May 1956 to May 1957. The expansion of the weasel population presumably was directly related to the expansion of the *Microtus* population. Only 10% of the production was not accounted for (Fig. 1). The least weasel may itself serve as food for certain predators, such as the great-horned owl, the barn owl, long-tailed weasel, and domestic cat (Hall 1951), but no information was gathered on mortality of weasels during this investigation.

ENERGY LOSSES OF THE SECOND ORDER

The energy losses of the second order, due to respiration (fasting metabolism), nonassimilation of energy in the food, and the energy cost of maintaining the body under normal activity, can be further separated into energy losses available and unavailable to the biosphere. Energy losses available to the biosphere include the energy in fecal matter which is composed primarily of unassimilated food but also contains intestinal secretions and cellular debris. Energy in the feces would serve as the base for food chains of coprophagous organisms. The energy lost to the biosphere as heat derived from animal metabolism can be considered an increase in the positive entropy of the ecosystem.

Respiration loss (respiration energy/energy consumed) determined for each step of the food chain is as follows: Vegetation—15.0%, Mice—68.2%, Least Weasels—93.3%. The respiration coefficient for the vegetation may be underestimated as stated earlier; Transeau (1926) and Thomas & Hill (1949) suggest that it may run as high as 25-30%. The data confirm the statement of Lindeman (1942) that as energy passes through the trophic levels an increasing percentage is lost in respiration. It must be remembered that the percentages cited above for the mice and weasel were both determined as minimum metabolic rates and, therefore, indicate basic differences in the loss due to metabolism and not mere differences in activity. Taking activity into account would presumably act to increase the difference.

The energy consumed but not assimilated by *Microtus* and *Mustela* was measured in the digestion trials. Of the energy consumed, 10-18% was recovered in the feces of *Microtus* and 10% in the feces of *Mustela*.

When these losses were subtracted from the energy loss of the second order for each species, 14-22% of the energy consumed was unaccounted for in *Microtus* and all the energy loss was accounted for in the least weasel. It is highly unlikely that the energy loss in respiration and in the feces comprises the total energy losses in the organism. For instance, energy is also lost in the urine, in fermentation gases, and in specific dynamic action of feeding (energy used in the processes of food utilization). Estimates of the energy loss in the urine are 15% for cattle and 7% for rabbits after fecal losses are subtracted from the gross food energy (Brody 1945: 28), and the loss in specific dynamic action varies from 40% of the intake energy for lean meat, 15% for fat, and 6% for sucrose (Brody 1945: 61).

An additional energy loss not included above is the expense of normal body activity above rest. Very few investigators have been concerned with this maintenance cost according to Brody (1945), although he estimates that this loss is twice the basal metabolic rate. The minimum energy expended when the animal is confined and fasting (fasting metabolism) is known for *Microtus* and *Mustela* and was used to determine the loss of energy in respiration; but the energy used

by these animals as they live in their natural environment is completely unknown. This latter energy expense reduces the efficiency of conversion by widening the gap between energy intake and production. The maintenance losses are reflected in the coefficients of production. Plants are the most sedentary and have the highest coefficient, 94.3% (net production/gross production). The weasel is the most active, since it must hunt for its food, and probably has the highest maintenance cost, with a low coefficient, 2.2% (production/energy intake). Possibly the energy expense of hunting by the predator will vary with different densities of the prey population. *Microtus* which is primarily dependent on vegetative material could be expected to have a low cost of maintenance and to display a higher coefficient than that shown in the study (2.1% production/energy intake). If the total energy losses in respiration and in the feces plus hypothetical maintenance cost are added to the production, the energy used totals more than the energy consumed by both the *Microtus* and *Mustela* populations. The reasons for this discrepancy were not determined, but food consumption rates estimated in the laboratory possibly underestimate the true food consumption of the more active animals in the field.

Since the maintenance cost is irreducible, the percentage of energy converted to production will be highest when the birth of new animals and the growth rate of living animals are the highest. This surge of production can most easily occur when sources of high energy food are available. *Microtus* conforms to this model, since the young are born and the rate of growth is highest during periods of greatest growth of the vegetation. It would further increase the year-round efficiency of the population to have the lowest population density during the period of little or no production by plants since at that time the dangers of over-exploitation of the food supply would be greatest. A low density at times of low plant production is the usual observation in field studies of the population dynamics of *Microtus* (Blair 1940, Martin 1956, Greenwald 1957, and others).

Finally, *Microtus* appears, on the basis of energy relationships, to be a relatively unimportant component of the community. Even when the energy consumption of insects (estimated as approximately 24% of the net production) is added to that of the mice, only 25% of the net production of the plants is accounted for. Odum (1959) emphasizes the distinction between the herbivores which eat green plants directly and the delayed feeders which eat dead plant material. Apparently, in this stage of old field succession the major portion of the plant net production is directed through these decomposer food chains.

SUMMARY

The energy dynamics of the perennial grass-herb vegetation—*Microtus pennsylvanicus*—*Mustela vison* food chain of the old field community was studied from May 1956 to September 1957.

Solar insolation for the growing season, measured

at East Lansing, Michigan, totaled 94.2×10^8 Cal per ha in 1956.

Primary net production by plants was broken down into the following components: (1) production of tops, (2) production of roots, and (3) consumption by *Microtus*. The net production of vegetation for 1956 was 49.5×10^6 Cal per ha and for 1957 was 44.3×10^6 Cal per ha. Respiration of the vegetation during the growing season amounted to approximately 15% of the net production, determined by crude field calorimetry. Gross primary production ranged from 58.27×10^6 Cal per ha in 1956 to 53.01×10^6 Cal per ha in 1957.

Population dynamics and weight changes of the *Microtus* population were studied by live-trapping. Tissue production of young and adult mice was 5,170 Cal per ha per yr. The fasting metabolic rate of mice determined in the laboratory was approximately 10 Cal per mouse per day. Energy lost to respiration equalled 169,877 Cal per ha per yr. The total energy used in growth of the weasel population were 130 Cal per ha per yr and in respiration, 5,434 Cal per ha per yr.

Stomach sample analysis indicated that *Microtus* ate primarily green grass and herbs. Weasels were assumed to feed predominantly on *Microtus*. Total yearly food consumption of the study area as determined from laboratory experiments, was 250,156 Cal per ha for *Microtus* and 5,284 Cal per ha for *Mustela*.

Of the solar energy available during the growing season, the vegetation used 1.2% in gross production and 1.1% in net production. These results compared favorably with the coefficients for primary production of terrestrial and aquatic communities determined by other workers. Of the energy available to the mice, 1.6% was consumed and 1.1% was utilized in growth and respiration. The weasel population consumed 31% of the energy available to it in the form of *Microtus*, and used 30% of the energy consumed in growth and respiration.

Twenty-one % of the production of the *Microtus* population and only 10% of the weasel production was lost from the food chain. These losses were diverted to other food chains through other predators or through micro-organisms.

Of the energy consumed only a portion was used in production; most of the energy went to respiration or passed through the digestive tract unused. Respiration cost increased from the vegetation level to the carnivore level of the food chain. The gross energy in the experimental diets which was recovered in the feces amounted to 10-18% for *Microtus* and 10% for *Mustela*.

LITERATURE CITED

- Bailey, V. 1924. Breeding, feeding and other life habits of meadow mice (*Microtus*). Jour. Agr. Res. 27: 523-536.
- Baker, J. R. & R. M. Ranson. 1932. Factors affecting the breeding of the field mouse (*Microtus agrestis*) Part 1. Light. Proc. Royal Soc. London (B) 110: 313-322.
- Baten, W. D. & A. H. Eichmeier. 1951. A summary of weather conditions at East Lansing, Michigan prior to 1950. Mich. State College Ag. Exp. Stat. 63 pp.
- Beckwith, S. L. 1954. Ecological succession on abandoned farm lands and its relationship to wildlife management. Ecol. Monog. 24: 349-376.
- Blair, W. F. 1940. Home range and population of the meadow vole in southern Michigan. Jour. Wildlife Mangt. 4: 149-161.
- . 1948. Population density, life span, and mortality rates of small mammals in the bluegrass meadow and bluegrass field associations of southern Michigan. Amer. Midland Nat. 40: 395-419.
- Bole, B. P., Jr. 1939. The quadrat method of studying small mammal populations. Cleveland Mus. Nat. Hist. Sci. Publ. 5(4): 15-77.
- Brody, S. 1945. Bioenergetics and growth. New York: Reinhold Publ. Corp. 1023 pp.
- Burt, W. H. 1948. The mammals of Michigan. Ann Arbor: Univ. Mich. Press. 288 pp.
- Clarke, G. L. 1946. Dynamics of production in a marine area. Ecol. Monog. 16: 321-335.
- Clarke, G. L., W. T. Edmondson & W. E. Ricker. 1946. Mathematical formulation of biological productivity. Ecol. Monog. 16: 336-337.
- Crabb, G. A., Jr. 1950a. Solar radiation investigations in Michigan. Mich. Agr. Expt. Sta. Tech. Bull. 222. 153 pp.
- . 1950b. The normal pattern of solar radiation at East Lansing, Michigan. Mich. Acad. Sci., Arts, and Letters 36: 173-176.
- Daubenmire, R. F. 1947. Plants and Environment. New York: J. C. Wiley Co.
- Davis, D. E. 1956. Manual for analysis of rodent populations. Ann Arbor, Mich.: Edwards Bros. 82 pp.
- Davis, D. H. S. 1933. Rhythmic activity in the short-tailed vole, *Microtus*. Jour. Anim. Ecol. 2: 232-238.
- Dice, L. R. 1922. Some factors affecting the distribution of the prairie vole, forest deer mouse, and prairie deer mouse. Ecology 3: 29-47.
- Eadie, W. R. 1952. Shrew predation and vole populations on a localized area. Jour. Mammal. 33: 185-189.
- Evans, F. C. & S. A. Cain. 1952. Preliminary studies on the vegetation of an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich. 51: 1-17.
- Fernald, M. L. 1950. Gray's Manual of Botany. 8th Ed. New York: Amer. Book Co.
- Greenwald, G. S. 1957. Reproduction in a coastal California population of the field mouse *Microtus californicus*. Calif. Univ. Pubs. Zool. 54: 421-446.
- Hall, E. R. 1951. American weasels. Kans. Univ. Pubs. Mus. Nat. Hist. 4: 1-466.
- Hamilton, W. J., Jr. 1937. The biology of microtine cycles. Jour. Agr. Res. 54: 779-790.
- . 1941. Reproduction of the field mouse, *Microtus pennsylvanicus* (Ord.). Cornell Univ. Agr. Expt. Sta. Mem. 237.
- Hatfield, D. M. 1935. A natural history study of *Microtus californicus*. Jour. Mammal. 16: 261-271.

- . 1939. Rate of metabolism in *Microtus* and *Peromyscus*. *Murrelet* 20: 54-56.
- . 1940. Activity and food consumption in *Microtus* and *Peromyscus*. *Jour. Mammal.* 21: 29-36.
- Hatt, R. T. 1930. The biology of the voles of New York. *Roosevelt Wildlife Bull.* 5(4): 509-623.
- . 1940. The least weasel in Michigan. *Jour. Mammal.* 21: 412-416.
- Korschgen, L. J. 1957. Food habits of coyotes, foxes, house cats, and bobcats in Missouri. *Missouri Fish and Game Div. P-R Series No. 15.* 63 pp.
- Lantz, D. E. 1907. An economic study of field mice. *USDA Biol. Surv. Bull.* 31: 1-64.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399-418.
- Linduska, J. P. 1950. Ecological landuse relationships of small mammals on a Michigan farm. *Mich. Dept. Cons. Game Div., Lansing.* 144 pp.
- Llewellyn, L. M. 1942. Notes on the Alleghenian least weasel in Virginia. *Jour. Mammal.* 23: 439-441.
- Martin, E. P. 1956. A population study of the prairie vole (*Microtus ochrogaster*) in northeastern Kansas. *Kans. Univ. Pubs. Mus. Nat. Hist.* 8(6): 361-416.
- McCay, C. M. 1949. Nutrition of the dog. Ithaca, N.Y.: Comstock. 337 pp.
- McLagen, N. F. & M. M. Sheahan. 1950. The measurement of oxygen consumption in small mammals by a closed circuit method. *Jour. Endocrin.* 6: 456-462.
- Merrill, A. L. & B. K. Watt. 1955. Energy value of foods—basis and derivation. *USDA Agr. Handbook No. 74.* 105 pp.
- Morrison, F. B. 1949. Feeds and Feeding. Ithaca, N.Y.: Morrison Publ. Co. 21st Ed. 1207 pp.
- Morrison, P. R. 1948. Oxygen consumption in several small wild mammals. *Jour. Cell. and Compar. Physiol.* 31: 69-96.
- Noddack, W. 1937. Der Kohlenstoff im Haushalt der Natur. *Ztschr. f. Angew. Chem.* 50: 505-510.
- Odum, E. P. 1959. Fundamentals of Ecology. 2nd. Ed. Philadelphia: Saunders. 546 pp.
- Odum, H. T. 1956. Efficiencies, size of organisms, and community structure. *Ecology* 37: 592-597.
- Park, T. 1946. Some observations on the history and scope of population ecology. *Ecol. Monog.* 16: 313-320.
- Pearsall, W. H. & E. Gorham. 1956. Production ecology. 1. Standing crops of natural vegetation. *Oikos* 7(2): 193-201.
- Pearson, O. P. 1947. The rate of metabolism of some small mammals. *Ecology* 28: 127-145.
- Polderboer, E. B. 1942. Habits of the least weasel (*Mustela vison*) in northeastern Iowa. *Jour. Mammal.* 23: 145-147.
- Regnier, R. & R. Pussard. 1926. Le campagnol des champs (*Microtus arvalis* Pallas) et sa destruction. *Ann. des Epiphyt.* 12(6): 385-535.
- Ricker, W. E. 1946. Production and utilization of fish populations. *Ecol. Monog.* 16: 373-391.
- Shively, S. B. & J. E. Weaver. 1939. Amount of underground plant materials in different grassland climates. *Nebr. Univ. Conserv. Bull. No. 21.* 67 pp.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16: 284-307.
- Terrien, J., G. Truffaut, & J. Carles. 1957. Light, vegetation and chlorophyll. New York: Philosoph. Libr. 228 pp.
- Thomas, M. D. & G. R. Hill. 1949. Photosynthesis under field conditions. In: *Photosynthesis in Plants*, edited by J. Franck and W. E. Loomis. Ames: Iowa State Col. Press. 500 pp.
- Toner, G. C. 1956. House cat predation on small animals. *Jour. Mammal.* 37: 119.
- Townsend, M. T. 1935. Studies on some of the small mammals of central New York. *Roosevelt Wildlife Ann.* 4: 6-120.
- Transeau, E. N. 1926. The accumulation of energy by plants. *Ohio Jour. Sci.* 26: 1-10.
- Veatch, J. O., et al. 1941. Soil Survey of Ingham County, Michigan. *USDA Soil Survey Series* 1933, No. 36. 43 pp.
- Whitmoyer, T. F. 1956. A laboratory study of growth rate in young *Microtus pennsylvanicus*. Unpubl. Master's thesis, Mich. State Univ. 62 pp.
- Wolcott, G. N. 1937. An animal census of two pastures and a meadow in northern New York. *Ecol. Monog.* 7: 1-90.
- Wooster, H. A., Jr. & F. C. Blanck. 1950. Nutritional Data. Pittsburgh: H. J. Heinz Co. 114 pp.

PRIMARY PRODUCTIVITY AND LIMITING FACTORS IN THREE LAKES OF THE ALASKA PENINSULA

CHARLES R. GOLDMAN

Department of Fisheries, University of Michigan, Ann Arbor, Michigan¹

TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	207	Laboratory Preparation and Analysis	213
GEOGRAPHY	208	Radioactivity Determinations	213
THE LAKES	209	RESULTS	214
Brooks	209	The Primary Productivity of Brooks, Naknek	
Naknek	210	and Becharof Lakes	214
Becharof	210	Variation in Primary Productivity within	
METHODS USED FOR MEASURING PRIMARY		Brooks and Naknek Lakes	216
PRODUCTIVITY WITH C ¹⁴	210	Experiments on Nutrient Factors Limiting	
Lake Studies	210	Productivity	219
Nutrient Experiments by Culture	211	DISCUSSION	223
Sampling Schedule	213	SUMMARY	226
Methods of Plankton Sampling and Water		LITERATURE CITED	227
Chemistry	213		

INTRODUCTION

The lakes draining into Bristol Bay along the base of the Alaska Peninsula are nurseries for juveniles of the red salmon (*Oncorhynchus nerka* [Walbaum]) spawned in the lake tributaries. Other Alaskan Pacific salmon are also taken in the coastal fishery, but the reds (also called sockeyes or bluebacks) contribute most to making the local fishery one of the most valuable in the world. Fluctuations from year to year in the abundance of the red salmon have prompted many investigations, yet various aspects of its ecology remain imperfectly understood.

This investigation was planned to measure and compare the primary productivity of certain red salmon nursery lakes, and determine what factors were limiting. The opportunity to make the study arose through the interest of the United States Fish and Wildlife Service in ecological factors that affect the numbers and condition of young of this important species. Field work was conducted from the Brooks Lake Research Station, established in 1940, which provided living quarters and laboratory facilities. It is supplied primarily by amphibious aircraft. The principal objective of the Station is to determine how physical, chemical, and biological factors affect populations of red salmon in fresh waters.

Considerable evidence suggests that the abundance of this salmon is determined by conditions during its early life in fresh water (Barnaby 1944). Its growth in fresh water, although only a fraction of that achieved in the sea, is of great importance in determining the percentage of a given year class that reaches sexual maturity (Foerster 1954). That food supply is a limiting factor in some drainage systems is sug-

gested by the inverse relationship between the average growth rate of juveniles and their numbers, as found by Foerster (1944). Supporting this viewpoint are the inverse correlations between available zooplankton and size of red salmon populations noted by Ricker (1937). More recently, Nelson (1958), following the growth of red salmon juveniles and smolts in fertilized Bare Lake, found a closer relationship between their growth rate and the gross photosynthetic productivity of that Lake than might have been expected in view of the many environmental factors in addition to food supply.

A logical point to begin the study of food supply in a lake is at the level of the photosynthetic primary producers. These organisms are neither all restricted to photosynthetic production of organic matter, nor do they represent the only primary producers. The photosynthetic carbon fixation by phytoplankton and bacteria has, however, been demonstrated to represent the major part of the organic production in lakes. Chemosynthetic productivity is of secondary importance (Kuznetsov 1956). Changes and differences in this basic productivity within a single lake and between various lakes may be expected to influence, although not always directly, the rate of accumulation of organic matter in successive trophic levels. The natural fertility or lack of fertility and rate of primary production in standing waters are therefore of fundamental importance for understanding and comparing lakes as biological units.

Methods of measuring primary productivity by phytoplankton were developed in the 1920's. According to Steemann Nielsen (1952), the work of Atkins (1922, 1923) was the first attempt at indirect measurement of organic production in the sea. His estimates were based on loss of carbon dioxide and phosphate

¹ Present address: Department of Zoology, College of Letters and Science, University of California, Davis, California.

from the water as it was taken up by phytoplankton. Earlier biologists had relied on direct measure of the standing crop, which, by its static nature, was of limited use in understanding a system constantly undergoing change. A very important step in measuring the rate of photosynthesis was development of the oxygen technique, apparently first used by Pütter (1924) and then by many others, including Gaarder & Gran (1927), Schomer & Juday (1933), Vinberg & Iarovitsina (1939), Riley (1940), Nygaard (1955), and Odum & Odum (1955). Chlorophyll content also has been used to estimate photosynthesis by such workers as Manning & Juday (1941), Riley (1940, 1941), Gardener (1943), Gessner (1949), and Ryther & Yentsch (1957). Daily variations in chlorophyll content are complicating factors in this technique (Yentsch & Ryther 1957). Verduin (1956a) used pH change as still another method of measuring photosynthesis. A major step in increased sensitivity of measuring primary productivity in natural water was achieved with the development of the C^{14} technique by Steemann Nielsen (1951, 1952). The relative merits of the oxygen, CO_2 , nutrient uptake, C^{14} , and chlorophyll methods of measuring primary productivity are reviewed by Ryther (1956).

Paralleling the advance in techniques was growth in appreciation of the complexities of organic transfer through aquatic systems. From the first consideration of the lake as a microcosm (Forbes 1887) through the early diagrammatic representation of food webs (Shelford 1913, Naumann 1925, Perfiliev 1929, MacFadyen 1948) to the trophic dynamic approach of Lindeman (1942) and estimates of "bioactivity" by Ohle (1956), there has been an evolution in understanding the complexity of energy transfer through the ecosystem. The early work of Lindeman provided a very important basis for development of the concept of productivity, although his trophic levels were criticized by Ivlev (1945) as an oversimplification of natural producer-consumer relations.

Confusion has arisen in the use of the words "production" and "productivity," because there has been a tendency to carry along in their meaning the static and deep-rooted concept of biomass. Thienemann (1931), the first to assess the terminology critically, was confused by considerations of energy and matter. Ivlev (1945) thought it inadvisable to use "potential productivity" because it does not reflect the existing state of the body of water in question. This confusion of biomass and energy was generally clarified by MacFadyen (1948) and Dussart (1950). MacFadyen suggested abandoning the term "production" and using "productivity" when speaking of the rate of flow of matter. In the present study, "primary productivity" is used as the net rate of fixation of organic carbon by bacteria and phytoplankton in photosynthesis. During the summer of 1957, I made the first comparative measurements of primary productivity in three red salmon nursery lakes of the Alaska Peninsula with emphasis on physical and chemical factors which were limiting the process.

Drs. K. F. Lagler and G. H. Lauff provided advice and encouragement during this investigation. Drs. D. C. Chandler, L. B. Slobodkin, and J. W. Moffett helped throughout the study and criticized the manuscript. Drs. L. Provasoli and W. Rodhe also provided helpful advice. Dr. W. F. Royce, U. S. Fish and Wildlife Service, established support of field activities under the Bureau of Commercial Fisheries Salmon Survival Investigations in Alaska. Field personnel at Brooks Lake, especially Director T. R. Merrell, R. E. Painter, and W. L. Hartman, helped with the field work. A grant from the Horace H. Rackham School of Graduate Studies provided for the initial Carbon-14 counts. Dr. I. A. Bernstein furnished facilities and technical assistance in gas phase counting. The U. S. Fish and Wildlife Service, Ann Arbor, made the flame spectrophotometer determinations.

GEOGRAPHY

This study area is about 260 air miles southwest of Anchorage, at the base of the Alaska Peninsula, between latitudes 58° and 59° North and longitudes 157° and 154° West (Fig. 1). Except for Lake Becharof, all the work was accomplished within the Katmai National Monument (Fig. 1).

The local aquatic and terrestrial ecology has been profoundly influenced by its geological history. The eastern half of the Katmai Monument is a glaciated region with rugged young mountains and volcanoes of the Aleutian Range. Glaciers are numerous and some of the volcanoes are still active. To the west the land slopes with gentle irregularity beyond the borders of the Monument to Bristol Bay.

On both the eastern and western sides of the peninsula the drainage pattern is dendritic. The proximity of the Aleutian Range to the eastern side gives the streams a steep gradient over their relatively short course to the coast. A few, nearly attaining base level, meander back and forth in the temporary channels on the valley floor before entering the Shelikof Strait. To the west of the divide, although the initial pattern is similar, the streams thread down the longer U-shaped valleys to lakes or, like King Salmon River, directly into the Bristol Bay. The low land is poorly drained. Small natural ponds and beaver impoundments dot a considerable area of tundra. Mud flats occupy extensive reaches of the immediate coast line.

Although volcanic origins may be considered for lakes in such a region, Atwood (1911), in a survey of the peninsula, suggested that the four large lakes (Kukaklek, Naknek, Becharof, and Ugashik) in the northeastern portion of the peninsula owed their depth and outline, if not their existence, to ice gouging. He further pointed out that except for Ugashik, all were in valley courses leading from the mountains to the shores of Bristol Bay.

The eruption of 1912, originally attributed solely to Mount Katmai, is now believed to have included the eruption of Novarupta. The total upheaval was

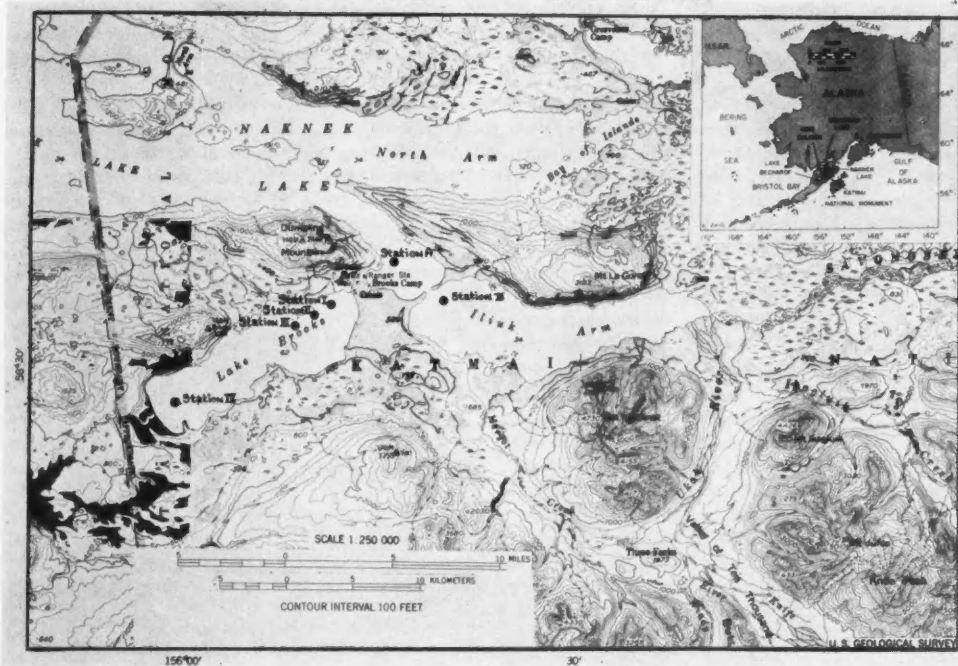


FIG. 1. Geographical location, study area, and sampling stations in the Katmai National Monument.

of great magnitude, flooding what is now called the Valley of Ten Thousand Smokes with more than a cubic mile of tuff (Fenner 1923), as well as depositing a great quantity of siliceous ash over a wide area. The Ukak River and its tributaries have now cut down through a hundred feet of this pumice and ash to form a narrow canyon. Since Robert F. Griggs led the first post-eruption expedition to the area, numerous geologists have visited the area to study the sequence of geologic events that marked the eruption.

Ecologically the area is of considerable interest. The furthest southwestward advance of the white spruce (*Picea glauca*) forests covers a good portion of the monument. This spruce together with cottonwood (*Populus deltoides* Marsh.), balsam (*Populus balsamifera* L.), alder (*Alnus*), and birch (*Betula*) grade gradually into the tall arctic reed grasses (*Calamagrostis* sp.), which in turn yield to the lichens, mosses, and a variety of small flowering plants of the tundra. Short stands of willows (*Salix* spp.) surround the multitude of tundra ponds to the south and west. On the gentler mountain slopes a variety of shrubs and bushes flourish.

The climate is warmer than might be expected at this latitude and is generally maritime in nature. The proximity of the Alaska Current to the east and the Bering Sea to the west have a stabilizing effect on the temperature, although continental air masses cause infrequent extremes. U. S. Weather Bureau climatological data for King Salmon, Alaska, are available since 1928. This is the government weather

station nearest to Brooks Lake which maintains complete records. A low of -45°F (-43°C) at Brooks Lake was recorded the winter of 1955-6. The average annual rainfall at King Salmon is 20.39 inches. During the summer of 1957 the 4-month total at Brooks Lake was 17% greater than at King Salmon. A comparison of summer rainfall at Brooks Lake and King Salmon since 1942 gives very similar values. Rainfall at Brooks Lake during June, July, August, and September averaged 1.87, 2.30, 5.31, and 3.64 in., respectively, during 1942-1957, exclusive of 1943, 1945, and 1946. Precipitation during the summer of 1957 was below these averages (United States Department of Commerce Weather Bureau 1957).

THE LAKES

BROOKS

Brooks Lake is 10.7 mi long and varies in width from 2.5 to 4.0 mi. The surface area, exclusive of islands, is approximately 28.2 sq mi (7308.5 hectares). It is 18.9 m above mean sea level, and the long axis lies northeast by southwest. There are three prominent islands in the lake with a total surface area of 66.4 ha. During the 1957 field season the depth of the basin was carefully ascertained with a Raytheon depth recorder. Morphometry was calculated by Olson's (1949) system. Maximum and mean depths were found to be 78 m and 45 m respectively. Shore development was 1.48. The northeast end has a broad, sandy littoral zone extending about a half mile from the shore. The other end of the lake has a similar

shelf of about half the width. The northwestern side of the basin drops off more rapidly than the southeastern, reflecting the greater proximity of the mountains to the west.

The general U-shaped basin of Brooks Lake is a smaller and perhaps somewhat deeper model of the other basins of probable glacial origin in the area. An area of over 12 sq mi of the lake has a depth of 61 m or greater, and an area of about 5 sq mi has a depth of 73 m or more. Mountains afford wind protection along the northwest and southwest sides. Both ends are open providing a maximum fetch for winds blowing in the direction of the long axis.

To the northeast, the Brooks River drains the lake into Naknek Lake, 9.2 m below. At the southwest end of Brooks Lake, Headwater Creek, its major tributary, meanders across a broad valley with only a slight gradient near its mouth. A number of small tributaries are found along both sides of the roughly rectangular lake. Those along the southeast side are typically clean, gravel bottomed streams which find their source in the small ponds and low lands at the base of the mountains. Although the five species of Alaskan Pacific salmon utilize these streams, Headwater Creek, and, to a limited extent, the lake shore for spawning, red salmon constitute the important spawning stock. The tributaries to the northwest are smaller and, for the most part, originate near the shore in beaver ponds or narrow gullies. During the 1956 and 1957 seasons, salmon were observed to spawn in only one of these streams.

NAKNEK

Naknek Lake, the largest body of water in the Monument, covers approximately 50,586 hectares at an elevation of 10.36 m. From the main lake, two arms extend to the east. The more northerly arm receives very little of the major drainage. The southerly Iliuk arm receives the outflow of Coville and Grosvenor lakes via the Savonoski River as well as the Ukak River drainage from glaciers and the Valley of Ten Thousand Smokes. Although complete soundings have not been made in the various parts of this lake, extensive areas of water less than 25 m in depth exist just off the mouth of the Brooks River. Contours based on 23 soundings in the southern portion of the lake (exclusive of the Iliuk arm) give an approximate mean depth of 20 m.

Both the Savonoski and the Ukak Rivers contain a great deal of suspended pumice and ash which reduces the transparency of Naknek Lake. The turbidity decreases progressively as one proceeds away from the tributaries toward the Naknek River outflow, but is still quite evident near the mouth of Brooks River where the inflow of clear water is in sharp contrast.

As mentioned previously, these lake basins appear to be the continuation of glacial valleys extending from the mountains to the east towards Bristol Bay. The Naknek Lake basin almost certainly has a deep deposit of pumice and ash from the eruption and from the tributary streams already noted. Rather

steep mountains rim the lake. The highest of these is Mount Katolinat, rising abruptly from the south shore of the Iliuk arm to an elevation of about 1402 m.

BECHAROF

Lake Becharof, second largest of Alaska's inland lakes, is approximately 50 mi south of Naknek. Its long axis is about 40 mi in a general east-west direction. The greatest north-south dimension is approximately 15 mi. The large Egegik River drains the lake into Bristol Bay, 35 mi to the west. The outlet, although a rapids strewn with boulders, is navigable to small boats. The lake's shoreline is more regular than that of Naknek Lake and lacks the rim of mountains except near the east end. It is beyond the advance of the white spruce forests and is bordered for the most part by a rocky shore with tundra beyond.

Soundings were taken to a distance of four miles east of the outlet. The bottom was rather flat and sandy in this area with a fairly uniform depth of about 25 m. Greater depths were encountered further east of the outlet. The drainage into the lake is through a number of small to moderate size tributaries.

METHODS USED FOR MEASURING PRIMARY PRODUCTIVITY WITH C^{14}

LAKE STUDIES

The C^{14} technique for measuring primary productivity of phytoplankton populations in natural waters, first presented by Steemann Nielsen (1951), involves the addition of a small amount of radioactive carbon as sodium carbonate to water samples contained in clear glass bottles. Determination of the amount of carbon fixed is based on the assumption that rates of photosynthetic fixation of C^{14} and C^{12} differ only slightly because of the slower uptake of the heavier, radioactive isotope of carbon. This difference of 6%, called isotope effect, is corrected for in the calculations. Because preliminary experiments indicated that non-photosynthetic uptake of C^{14} exceeded the 1% of photosynthetic uptake suggested by Steemann Nielsen (1952), dark bottles were included with each experiment at selected depths at all stations to measure this. For the short incubation periods used it is assumed that dark uptake of C^{14} can be used as an estimate of nonphotosynthetic uptake in the light.

Water samples were collected from selected depths at each station and transferred to 150 ml, clear, glass-stoppered bottles. When all the samples for an experiment were on hand, five microcuries of C^{14} were added to each sample bottle. The sodium carbonate was prepared by Volk Radio Chemical Company, Chicago, in 100 ml serum bottles with an activity of 2.5 microcuries per ml. An automatic hypodermic syringe (Cornwall No. 1251 B D) was adapted to facilitate its rapid injection into the 150 ml, clear, glass-stoppered bottles without danger of contamination (Fig. 2). This procedure allowed a minimal

time lapse for C^{14} addition among the bottles at each station and among stations. The time of C^{14} addition was carefully noted so that the isotope would be available to the algae for the same interval in each bottle. Each of these bottles had a metal snap tied to its neck for ease of attachment to hog rings secured at measured intervals to a line which, in turn, was attached to a float at each permanent station.



FIG. 2. An automatic hypodermic syringe was adapted to facilitate rapid injection of $Na_2C^{14}O_3$ into sample bottles.

In Brooks Lake the three main study stations were located over depths of 5 m (Station I), 35 m (Station II), and 65 m (Station III), and were as representative as possible of the lake as a whole. The sites were marked by well-anchored buoys. Each float was made from an inflated automobile inner tube securely lashed to a wooden crosspiece. A portable float of the same construction was also utilized as a supplementary station at the south end of Brooks Lake as well as in Naknek Lake and Lake Becharof.

Sample bottles were suspended at one-meter intervals from the surface to 5 m at all stations. At Stations II and III bottles were also placed at 10, 15, 20, 25, and 35 m. In addition, Station III had bottles at 50 and 65 m. After four hours, the bottles in each series were retrieved and placed in a light-proof, insulated wooden box in which they were transported without delay to the laboratory for prompt filtration.

Filtering equipment included a 110-volt centrifugal vacuum pump connected to six vacuum flasks. Each flask had a funnel which was fitted to a coarse porosity, fritted glass disk. Funnel and disk were held securely together by a spring-loaded clamp. A pre-cut, 3.016 cm HA Millipore filter (Millipore Filter Corporation, Watertown, Massachusetts) was sealed between the funnel and the disk by the pressure of the clamp. The $0.45 \pm .02$ micron HA Millipore filter was selected because of its ability to retain the nanoplankton (Goetz & Tsuneishi 1951; Goldberg *et al.* 1952). Because of activity loss through filters,

a porosity of at least 0.45 microns was recommended by Lasker & Holmes (1957).

Light meter readings, Secchi disk depths, and temperatures were recorded at each sampling period. To insure uniform light exposure, the sample bottles were taken one at a time from the lightproof insulated dark box and treated in the following manner. After shaking the sample to resuspend any settled plankton, 100 ml were pipetted into the funnel and filtered at a maximum vacuum of 15-20 in. Hg. Two ml of a pale blue Janus Green B dye solution were added to the sample to show whether or not leakage occurred over the edge of the filter.

After the sample was filtered, 10 ml of .003 N HCl were pipetted onto the filter to remove any residual carbonate adhering to it or to the organisms and to wash any organisms from the surface of the funnel to the filter. Addition of 10 ml of 3% formalin for preservation of the organisms followed. Then the funnel was removed and the wet filter placed in a labeled aluminum sample pan of 3.18 cm diameter. After desiccation, the filter was glued to the pan with a thin film of nitrate dope and stored for subsequent counting.

Because radiation counting equipment was not available at the Brooks Lake Station selected samples were air-mailed to Ann Arbor, Michigan, for counting during the field season. The rest were stored and counted later. The results of the radioactivity determinations on the mailed lots were obtained within two weeks and provided a quality control for the field operations.

To assess total experimental error, duplicate samples were taken at each station once during the period of field operations. Each procedure was duplicated including the collection of two separate water samples at each depth, the preservation of separate plankton samples, etc. A simple wire harness was attached at each level so that the two samples could be suspended at exactly the same depth during the experimental period.

NUTRIENT EXPERIMENTS BY CULTURE

The sensitivity of culture techniques for determining the availability of nutrients for phytoplankton growth has been recognized for many years. Schreiber (1927) working with sea water, Ström (1933) using Schreiber's approach in fresh water, Chu (1942), Edmondson & Edmondson (1947), Rodhe (1948), Potash (1956), and Provasoli *et al.* (1957), to name a few, have developed and used culture techniques with considerable success.

Phytoplankton population growth has been measured most frequently by direct cell counts (Serfling 1949), although light extinction coefficients (Åberg & Rodhe 1942), chlorophyll (Ryther & Yentsch 1957), volumetric, and gravimetric measurements have also been used. The low plankton concentrations encountered in the natural Alaskan waters used as media rendered all these techniques less applicable than the C^{14} method already discussed (Stemann

Nielsen 1955). Therefore, the main experiments in this study involved a comparison of the rate of carbon assimilation in the different cultures. The measurement of growth was not dependent upon a significant increase in cell numbers during the culture period, but rather upon an increase in the rate of photosynthetic accumulation of organic carbon which may not be immediately manifest in a numerical increase. The extreme sensitivity of this technique for detecting nutrient limiting factors was demonstrated by the author in the laboratory before the field work was undertaken.

During the summer of 1957, 14 culture experiments were conducted. In most of them, lake water with its natural plankton population (chiefly green algae and diatoms) was placed in gallon or half-gallon jars in a floating crib near the lake outlet. Thus, the cultures were at lake surface water temperature and light conditions, and the constant rocking of the crib by current and wave action helped keep the algae in suspension. Cultures were moved daily from place to place within the crib to eliminate any variability due to position. Vitamins B₁ and B₁₂, KH₂PO₄, Na₂CO₃, MnSO₄, MgSO₄, Ca(NO₃)₂, and a variety of oligoelements (Fe, Cu, Zn, and Co) chelated with EDTA (ethylenediamine tetra-acetic acid), as used by Provasoli & Pintner (1953), were tested separately and in certain combinations to determine which were most limiting. Other culturing was done with Brooks Lake water shipped to the laboratory in gallon polyethylene bottles. In addition to the above mentioned chemicals, Mg(NO₃)₂, NaNO₃, Na₂SO₄, CaSO₄, K₂SO₄, and K₂HPO₄ were used in these cultures.

Bottom sediment extract was also assayed in order to determine its value as a phytoplankton nutrient. This extract was prepared from a sample of the bottom sediment collected at Station II. A volume of 400 ml was thoroughly mixed with an equal amount of lake water and allowed to settle for several hours. The liquid was then decanted and centrifuged twice in a Foerst Constant Speed Centrifuge. As a final treatment to remove microplankton and bacteria, the extract was passed through HA Millipore filters. After analysis for phosphorus, nitrite, alkalinity, hardness, hydrogen-ion concentration, and silica, the filtrate was added to cultures in different percentages by volume. One or more controls were maintained with these as with all culture experiments.

Lake water for the culture media was collected from the surface at Station I. After careful mixing, the total sample was divided into subsamples in 1 gal. or 1/2-gal. glass jars. Three liters of lake water were used in the former size and 1.0 or 1.5 liters in the latter.

A measure of the rate of production in the cultures was accomplished by further subsampling with the addition of C¹⁴. One hundred ml of each culture were pipetted into a 125 ml glass stoppered bottle after first shaking the jar to insure uniformity of plankton distribution. When all these subsamples had been taken, 2.5 microcuries of C¹⁴ were added to

each. The sample bottles were then suspended in the river from a line stretched perpendicular to the direction of river flow in such a manner that the bottles remained just beneath the surface. One or more dark bottles were included as a measure of non-photosynthetic uptake of C¹⁴. After a four-hour incubation period, samples were filtered and their radioactivity was measured in the same manner as the lake samples. To be certain that the addition of C¹⁴ as Na₂CO₃ was not altering the rate of photosynthesis, the oxygen method of measuring photosynthesis was used under controlled conditions. Various concentrations of Na₂C¹⁴O₃ up to the highest quantity used in lake or culture experiments were tested. Rate of oxygen production was not measurably altered by the addition of sodium carbonate.

In mixed algal populations it is possible that the presence of one species may inhibit the growth of another (Akehurst 1931, Lefevre *et al.* 1949). Pratt (1943), on follow-up work with growth inhibiting substances from *Chlorella vulgaris*, demonstrated the inhibitory effect of this substance on *Chlorella pyrenoidosa* as well as on mixed algal cultures. Rice (1954) and Proctor (1957) showed the existence of similar antimetabolites with a number of different species of algae. In order to learn whether or not such an effect was extant in these experiments, unialgal culture series were conducted to eliminate possible interaction for comparison with cultures utilizing the natural lake plankton populations. A pure culture of the green alga, *Ankistrodesmus falcatus* (Rodhe), was obtained on proteose agar from the Algae Bank of the Indiana University Department of Botany. From this pure lot, the sterile Culture Solution VIII of Rodhe (1948) was inoculated.

The lake water used as a culture medium for the unialgal experiment was prepared by passing 10 liters of surface water from Station I through a Millipore filter, thus removing bacteria, algae, and particulate matter. A liter of the filtrate was then placed in each of nine two-quart culture jars. After filtering the *Ankistrodesmus falcatus* from Rodhe's Solution VIII, the algae were washed with and resuspended in distilled water. Following the addition of six ml (approximately 10⁸ cells) to each culture, various nutrients were added. Periodic sampling of these cultures was accomplished in the manner already described, with one exception. Because of the smaller culture volume, only 50 ml subsamples of each were incubated. The C¹⁴ was correspondingly reduced to 1.25 microcuries. In this experiment, as in the others, duplicate samples of cultures were taken to determine the experimental error of the techniques employed. *Ankistrodesmus falcatus* was again used in subsequent pure culture experiments in the laboratory at Ann Arbor, Michigan.

It has been suggested that results of culture experiments may not be readily applied to the natural environment because restriction of plankton in a container does not duplicate the natural conditions and may favor the development of atypical forms. To

offset this, in addition to using the natural lake plankton, every attempt was made to duplicate the natural lake light and temperature conditions in the experimental cultures. However, to strengthen the findings, a test was conducted in the lake itself of nutrients found to be limiting. Since direct application of nutrients to the lake as a whole was not possible and because the C^{14} technique was sufficiently sensitive to rapidly detect changes in the rate of photosynthesis, short term nutrient experiments were conducted at Station I.

SAMPLING SCHEDULE

Radioactive carbon experiments were conducted from the first half of June to September, 1957, with reduced sampling to October. Lake studies were run every five days at the three permanent Brooks Lake stations simultaneously. A diurnal study was also initiated to determine variation in the daily photosynthetic rate. Naknek Lake was sampled every 15 days, and the south end of Brooks Lake at least once a month. Single comparative measurements were made in both Lake Becharof and the Iliuk arm of Naknek Lake. One to three culture experiments were continuously in progress during the summer.

METHODS OF PLANKTON SAMPLING AND WATER CHEMISTRY

During the regularly scheduled C^{14} lake experiments, plankton was sampled by collecting 250 ml of water from the same samples used for the C^{14} uptake measurements, and by taking vertical hauls with a #20 Wisconsin closing net. During the first two sampling periods plankton were collected at each C^{14} sampling depth. After this they were taken on alternate C^{14} sampling dates (*i.e.* every ten days) at the surface and at depths of 5 m at each station, 35 m at Station II, and 35 and 65 m at Station III. On the alternate sampling days, vertical hauls were made with the Wisconsin closing net.

A 10-day schedule at the three permanent Brooks Lake stations was also established for chemical water analysis, Clarke-Bumpus plankton tows, and centrifuge plankton samples. Depths for this schedule were surface and 5 m at Stations I, II, and III, 10 and 25 m at Stations II and III, and 35 and 50 m at Station III.

LABORATORY PREPARATION AND ANALYSIS

From the 250 ml water samples taken for plankton analysis during the lake productivity experiments, 100 ml were preserved by adding formalin to make a 3% solution for inverted microscope analysis and another 100 ml were filtered on a gridded Millipore filter. To achieve a more random distribution of plankton on the filter than could be obtained with the funnels used for C^{14} filtering, 0.875 in. inside diameter cylinders of plexiglass were fitted with flanges so that they could be clamped directly to the fritted disks of the vacuum system. After washing down any organisms adhering to the sides of the cylinders

with 3% formalin, the filters were placed on clear, labeled, microscope slides and allowed to dry several hours in a dust free environment. After drying, the filters were cleared with two drops of cedarwood oil and one drop of terpineol. Mounting medium and a number one cover slip were then added. Vertical haul plankton samples were preserved immediately with formalin.

Two liters of water from each sampling depth were centrifuged in a Foerst Constant Speed Centrifuge. The sample was then placed in a calibrated centrifuge tube and hand centrifuged. After a wet volume determination was made, the sample was resuspended by shaking and subsamples were placed in a Sedgwick-Rafter Counting Chamber for identification and enumeration of organisms.

Water analyses included the determination of phosphate, nitrite, silica, turbidity, dissolved oxygen, pH, alkalinity, and total hardness. Photocolorimetric determinations in ppm were made for phosphate, nitrite, and silicon, using standard procedures outlined in the Klett-Summerson photoelectric colorimeter "Industrial Manual."

Turbidity measurements were made with the colorimeter until 24 July when a Hellige turbidimeter became available. The early values were then converted to the Hellige readings. The Hellige turbidimeter, sensitive to turbidity ranges below .80 ppm SiO_2 , was more satisfactory than the Klett-Summerson because of the low turbidity encountered in Brooks Lake.

Total hardness determinations were made with a "BKH Water Hardness Outfit." Hydrogen-ion concentration values were obtained with a Hellige pocket comparator, glass disk type, using bromthymol blue-D indicator. Oxygen content was measured by the unmodified Winkler method as nitrogen was below 0.1 ppm (American Public Health Association *et al.* 1955). Water shipped to Ann Arbor in polyethylene containers was analyzed by flame spectrophotometer for magnesium, sodium, potassium, and calcium.

Alkalinity was determined by titration using methyl orange indicator. Available carbon determinations, essential for calculations of photosynthetic rates in C^{14} experiments, were based on total alkalinity, pH, and the dissociation constants of Hutchinson (1957). Actual conversions of pH and alkalinity to available carbon were made from a convenient table by R. W. Bachmann (unpublished).

RADIOACTIVITY DETERMINATIONS

The validity of conclusions based on the measurements of radioactivity depends upon the accuracy of the correction of errors in counting and, since no machine detects all the disintegrations, on the degree of accuracy attained in determining the efficiency of the machine employed. There is a definite probability at any given time of a nucleus disintegrating regardless of the atom's environment. The rate of disintegrations (which register as counts) therefore follows either a normal or a Poisson distribution (Lapp & Andrews 1955). Because the standard deviation

closely approximates the square root of the total counts, the desired accuracy can easily be achieved by adjusting the counting time. In this study samples were counted to $\pm 3\%$ or better.

Natural cosmic and machine radiation must also be corrected for. Since samples from dark bottles were always included in the experiments reported here, these samples not only served to measure counts from non-photosynthetic uptake by chemosynthesis (chemolithotrophy) or absorption, but also served as a basis for subtracting machine and sample background as well. Thus, in one subtraction all background and non-photosynthetic uptake could be eliminated without the necessity of determining these factors individually.

In determining the amount of C^{14} assimilated in photosynthesis it is necessary to know how much C^{14} was available. The $Na_2C^{14}O_3$ used was prepared with an activity of 2.5 microcuries per ml. This absolute activity was based on a National Bureau of Standards calibrated source with an accuracy of $\pm 10\%$. The error involved in preparing the $Na_2C^{14}O_3$ in 100 ml serum bottles was only about $\pm 0.3\%$.

As noted above, the C^{14} technique necessitates conversion of detected counts to absolute counts. Steemann Nielsen (1952) filtered barium carbonate- C^{14} of known activity onto a collodion filter and plotted a self-absorption correction curve. On the assumption that the geometry of the filtered barium carbonate was identical with the geometry in measuring the activity of filtered plankton, and because the weight of the plankton was always below 0.1 mg per three sq. cm, the activity of plankton could be directly compared with barium carbonate of known activity. Self-absorption in the plankton was therefore disregarded.

Because of the low energy Beta emission of the C^{14} atom (0.155 Mev), I felt that self-absorption should not be ignored nor should a counting efficiency be based on a barium carbonate standard if a better one could be devised. To circumvent these problems, my calibration was based on filtered algae of known activity. To prepare and calibrate this source, duplicate samples of the alga, *Ankistrodesmus falcatus*, and nanoplankton grown in a C^{14} rich medium were killed with formalin, filtered, washed, and resuspended in distilled water.

One set of the duplicate samples was desiccated in flasks, burned to CO_2 (Van Slyke & Folch 1940), and counted in accordance with the gas phase counting method of Bernstein & Ballentine (1950). The high efficiency gas phase counts were then converted to absolute counts with an efficiency value determined by combusting and counting a number of calibrated samples (Series A, June 1949, S. S. No. GS3849, PO No. 155382, National Bureau of Standards).

Quadruplicate samples, taken for the second set, were Millipore filtered, desiccated, and counted with the same equipment used for all the experimental counts. The algae suspension was sufficiently dilute to provide single cell thickness on the filters. The true efficiency of the equipment used in counting an

algal source of known activity could thus be obtained by comparison with the gas counts. By removing the C^{14} from the algae and counting it as CO_2 , the problems of self-absorption and geometry have been eliminated.

The replicated samples from gas conversion counts and Millipore filter counts allowed a statistical evaluation of the ratio derived (Arkin & Colton 1953). This efficiency was equal to 31.63% with a standard deviation of $\pm 0.64\%$ (31.63 ± 0.20).

RESULTS

THE PRIMARY PRODUCTIVITY OF BROOKS, NAKNEK, AND BECHAROF LAKES

The need and the desire to classify lakes has long been a motivating force in limnology. In the past a great variety of geographical, physical, chemical, and biological criteria have been employed for this purpose with varying degrees of success. Recently Nygaard (1955) has added productivity to the list. Since productivity must necessarily be a synthesis of the host of variables acting in any lake, it is likely to emerge the most important. Nygaard, who compares his Compound Index with primary productivity measurements, points out the danger of predicting productivity with chemical measurements alone and the improbability of founding the concepts of oligotrophy and eutrophy exclusively on the basis of productivity.

In the study reported here, regular biweekly measurements of photosynthesis with C^{14} were made in Naknek Lake for comparison with the more intensive sampling in Brooks Lake. A single measurement in Lake Becharof was included because of the lake's size, importance, and decidedly different typology. Estimates of productivity on both a unit volume and surface area basis were possible because sufficient measurements were made at each sampling to construct a curve of the variation in photosynthesis with depth. By computing the total area under each curve by planimetry, the total carbon fixation in the euphotic zone was obtained. Mean productivity per unit volume was calculated by dividing this figure by the depth of the euphotic zone, and mean primary productivity per unit of surface area by multiplying the average productivity per m^3 by the depth of the euphotic zone or by the mean depth depending upon which value was lower. This is an important consideration if a meaningful comparison of primary productivity among lakes is to be made on a surface area basis. If the euphotic zone exceeds the mean depth, as was the case in Brooks Lake, the average surface area productivity is limited by the mean depth. In contrast, the estimated mean depth of Naknek Lake is greater than the euphotic zone. An areal estimate of productivity in this lake must therefore be restricted to the depth of the euphotic zone.

A marked diurnal variation in the rate of photosynthesis by plankton populations has been noted by Doty & Oguri (1957) and further investigated by Verduin (1957). A diurnal study was made at Brooks Lake, and the curve (Fig. 3) for the rate of carbon

fixation per hour formed the basis for converting the 4-hr measurements to daily net photosynthesis. Solar energy reduced to the photosynthetic range in Langley's per minute ($15^{\circ}\text{C gm-cal/cm}^2/\text{min}$) taken from Brooks Lake pyrhelimeter recordings during the diurnal study is also given.

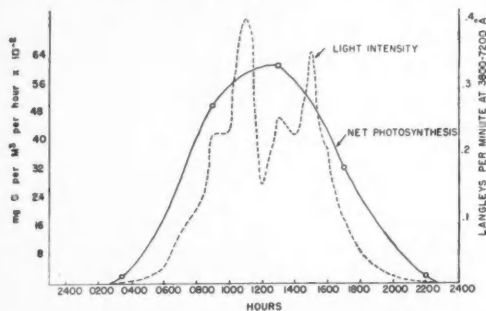


FIG. 3. Diurnal curves for the net rate of photosynthesis and pyrhelimeter values for variation in light intensity at Brooks Lake on 1 September 1957.

All measurements were corrected for seasonal variation in the visible portion of the spectrum (4000 Å to 7000 Å) penetrating a smooth water surface at sea level. The solar radiation values used were monthly averages of the U. S. Weather Bureau as compiled by H. B. Gotaas and W. J. Oswald (unpublished), interpolated to $58^{\circ}30'$ North latitude, and corrected for average monthly sunrise to sunset cloud cover during 1957 (Fig. 4). Average monthly cloud cover data were obtained for the King Salmon Weather Station ($58^{\circ}41'$ North, $156^{\circ}39'$ West) from the Weather Bureau, U. S. Department of Commerce.

The most striking feature of a comparison between the productivity of these lakes is the much higher rate per unit volume in Naknek Lake as compared with either Brooks or Becharof Lakes (Table 1). Because of the limited euphotic zone in the shallow south arm of Naknek Lake, and despite a rate of carbon fixation per unit volume over three times that of Brooks Lake and 17 times that of Lake Becharof, the difference in productivity per m^2 of surface area between Brooks and Naknek Lakes is not great. This has been generally recognized in other lakes (Ruttner 1952, Ohle 1956). No estimate for Lake Becharof is included because the mean depth is not known. On the basis of transparency, however, the euphotic zone probably exceeds 70 m at mid-day. The accuracy in estimation of the euphotic zone is dependent upon the degree of precision in determining the average "compensation point" (the place at which photosynthesis balances respiration; Jenkin 1937). This depth necessarily moves upward with decreases in light penetration and downward with increases. Estimates for compensation depth vary from 7 m at Woods Hole harbor to 100 m in the Sargasso Sea (Clarke 1954). Talling (1957) reviews the subject briefly in a formulation for "Respiration losses and the 'compensation point.'"

In Brooks Lake the vertical euphotic zone varied

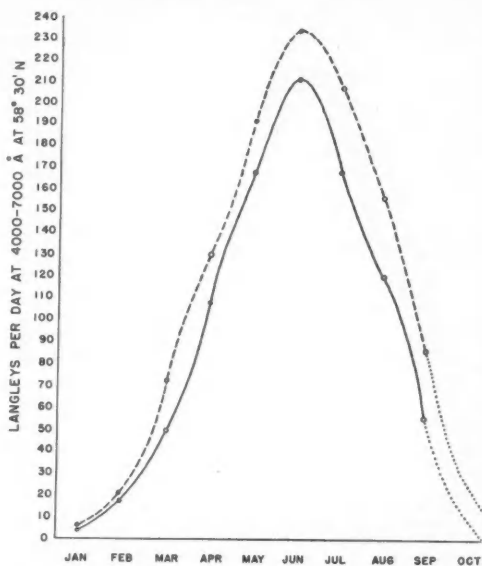


FIG. 4. Seasonal variation at $58^{\circ}30'$ North in the visible portion of the spectrum (4000 Å to 7000 Å) penetrating a smooth water surface at sea level. Solid line corrected for cloud cover; broken line not corrected for cloud cover.

in depth from about 25 to over 50 m, with an average of 46 m for the seasonal sampling periods. This is fortuitously close to the mean depth of 45 m which is used in this study for the areal estimate of productivity in the lake. The considerable difference in the rate of carbon fixation on a clear day as opposed to a rainy day is illustrated by Fig. 5. On these two days the $\text{mgC}/\text{m}^3/\text{day}$ is within about 10% of being proportional to the available light energy, as measured by pyrhelimeter. The production on the extremely cloudy day (17 August) corresponds to Nygaard's (1955) figure for reduction of light intensity to about 10% of that encountered on a bright day. In contrast to the deeper stations, Station I exhibited light inhibition (Edmondson 1956) on the bright day as evidenced by higher productivity on the dark day.

In Naknek Lake the minimum compensation depth was found to be about 14 m. Extreme fluctuations in transparency coupled with those of light intensity would extend this zone considerably on bright days if lake depth allowed. Strickland (1958) has noted that the steady compensation depth at noon will be only 4-5 m below the 24-hr mean compensation depth. Although the mean depth of Naknek Lake is not known, an estimate of 20 m was made from 23 soundings in approximately 60 sq mi of lake west of the Iliuk arm. All measurements of photosynthesis in Naknek Lake extended to 13 m and some to 17, and the depth of the euphotic zone averaged about 16 m; this depth was used for an approximation of carbon fixation per m^2 of surface area. Because sampling dates in Brooks Lake bracketed those in Naknek

TABLE 1. Rates of photosynthetic carbon fixation in three lakes of the Alaskan Peninsula in 1957.

NAKNEK ¹			BROOKS ²			BECHAROF	
Date	mg C/m ² /Day	mg C/m ² /Day	Date	mg C/m ² /Day	mg C/m ² /Day	Date	mg C/m ² /Day
20 June..... (10) ³	10.23	163.66	18 June (10)	3.80	170.90		
6 July..... (9)	14.05	224.80	3 July (8)	4.87	219.14		
20 July..... (5)	10.79	172.61	23 July (8)	4.19	188.73		
4 August..... (9)	8.71	139.43	2 August (2)	3.10	139.45		
19 August..... (4)	10.42	166.64	22 August (2)	1.96	88.07	23 August (2)	0.63
5 September... (9)	10.69	171.12	2 September (8)	3.19	143.64		
Mean.....	10.81	173.04		3.52	158.32		0.63
Experimental Error.....	± .09			± .16			

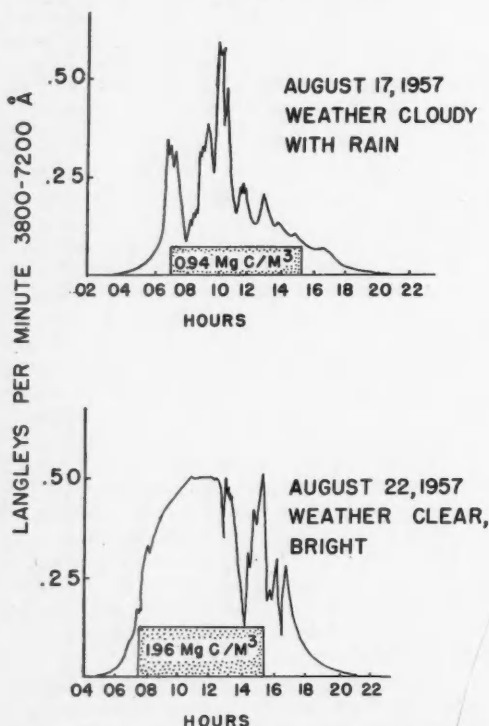
¹ Estimate of mean depth 20 m based on 23 soundings. Euphotic zone 16 m.² Mean of Stations II and III. Mean depth of Brooks Lake 45 m.³ Estimated cloud cover (10.0 equals complete cloud cover).

FIG. 5. Average net photosynthesis with variation in solar radiation at Brooks Lake Stations I and II. Lake, the dates showing the greatest similarity in weather conditions were used for comparison in Table 1.

The relationship of Secchi depth to the compensation point has received attention in the literature since Poole & Atkins (1929) calculated an approximate

ratio of 1.7/Secchi depth in meters for the extinction coefficient of visible rays. Verduin (1956b), in reviewing some of the literature on the subject, gives values of 2.5 to 5.0 times the Secchi depth for estimations of the compensation point. The ratio of the mean depth of the euphotic zone and the mean Secchi depth in Brooks Lake gives a factor of 3.6 with variation at least as great as those noted above. Naknek Lake, with an average Secchi depth of only 3.9 m, had a ratio of 4.5. This difference probably resulted from the human eye's being more sensitive to the longer wave lengths of a given light energy favored by turbid water (Sverdrup *et al.* 1942). The approximate nature of Secchi disk conversion factors may result in errors of 25% or more from variation in back-scattering of light encountered in natural waters (Strickland 1958).

VARIATION IN PRIMARY PRODUCTIVITY WITHIN BROOKS AND NAKNEK LAKES

The sites of Stations I, II, III, and IV (Fig. 1) were selected not only to provide a good average estimate of the primary productivity of Brooks Lake, but also to serve as an accurate comparison between different areas in the lake. The first three Brooks stations, each sampled 16 times during the summer, formed a matrix of 96 measurements for a comparison of carbon fixation in the first 5 m of Stations I, II, and III, 144 for the first 20 m of Stations II and III, and 176 measurements for the first 35 m of these last two stations.

For easier comparison with the four sampling dates at Station IV, these data have been arbitrarily grouped in Tables 2, 3, and 4 as the means of four consecutive dates covering each of four 15-day periods. This grouping of Stations I, and II, and III has the further advantage of combining a variety of light conditions since each group includes at least one bright day and never more than two.

TABLE 2. Rates of primary productivity in $\text{mgC}/\text{m}^3/\text{day}$ for the first 5 m of four Brooks Lake Stations. Measurements were made at Station IV on 26 June, 22 July, 15 August, and 6 September respectively.

Dates	Station I (5 meters)	Station II (35 meters)	Station III (65 meters)	Station IV (35 meters)
18 June to 3 July.....	4.59	4.85	5.55	3.89
8 July to 23 July.....	2.91	2.59	3.98	3.40
28 July to 12 August....	2.82	3.68	3.59	4.82
17 August to 2 September.....	2.52	2.70	3.31	5.55
Mean.....	3.21	3.45	4.11	4.42
Standard Error.....	.05	.05	.12	.19
No. of Measurements...	96	96	96	24

TABLE 3. Rates of primary productivity in $\text{mgC}/\text{m}^3/\text{day}$ in the first 20 m of three Brooks Lake Stations. Measurements were made at Station IV on 26 June, 22 July, 15 August, and 6 September respectively.

Dates	Station II (35 meters)	Station III (65 meters)	Station IV (35 meters)
18 June to 3 July.....	6.01	6.08	5.92
8 July to 23 July.....	2.45	4.80	4.40
28 July to 12 August.....	3.24	3.82	9.86
17 August to 2 September....	2.42	2.80	4.19
Mean.....	3.53	4.38	6.09
Standard Error.....	.07	.12	.14
No. of Measurements.....	144	144	39

Even preliminary comparison of sample radioactivity counts by variance analysis indicated a very significant statistical difference between stations. Although the average starting time differential between Stations I and III was only 20 minutes, this difference, because of peak photosynthesis about noon, was found to favor the earlier starting time. In the three comparative tables (2, 3, and 4), the values for Stations I, II, and III were corrected on the basis of the diurnal curve to the same starting time on each data before statistical comparison of the rates of productivity. This correction, although slightly reducing the differences between the three permanent stations, did not alter the trend or the significance of these differences.

The primary productivity at Station IV is only an approximate comparison because productivity measurements could not be taken there and at the three permanent stations on the same day. Meteorological conditions could therefore bias the results of sampling carried out on four dates. In this respect, it is of interest that two of the measurements were made on cloudy days and two on clear days.

In comparing the first five m of Stations I, II, and III, it is evident that a direct relationship exists between the average rate of primary productivity in the first five meters and the depth of the stations (Table 2). In addition and perhaps more important is the

TABLE 4. Rates of primary productivity in $\text{mgC}/\text{m}^3/\text{day}$ in the first 35 m of three Brooks Lake Stations. Measurement made at Station IV on 15 August.

Dates	Station II (35 meters)	Station III (65 meters)	Station IV (35 meters)
18 June to 3 July...	4.45	4.85	
8 July to 23 July...	2.19	4.05	
28 July to 12 August.....	2.84	4.22	8.18
17 August to 2 September...	1.79	2.24	
Mean.....	2.82	3.84	8.18
Standard Error...	.05	.07	.21
No. of Measurements.....	176	176	12

trend for higher production per unit volume as one proceeds away from the outlet in the direction of the major tributaries.

When all 16 dates are compared, Station II is just significantly higher in production at the 0.05 level by Wilcoxon sum than Station I. Predominant WSW winds during July caused a concentration of plankton in the vicinity of Station I. If the four measurements in July are excluded the difference is significant at the 0.01 level.

When Station II is compared with Station III the degree of significance by the same test increases to the 0.025 level. The greatest difference (significant at the 0.01 level) is obviously between Stations I and III. This trend in higher production rates is retained by Station IV.

A comparison of the first 20 m of the three stations yields very similar results to a comparison of the first 5 m (Table 3). Station IV again retains the trend, even if the unusually high productivity of 8 August were excluded from the average. The difference in productivity per unit volume between the first 5 m and the first 20 m of Stations II and III is not significant.

A decrease in average productivity per m^3 is evident when an additional 15 m of depth is included in the comparison (Table 4). Station III is consistently more productive in the first 35 m than Station II, at a significance level of 0.005. The only date when measurements extended to a depth of 35 m at Station IV was 15 August. This was a bright day and the warmest of the summer, with a record high of 83°F recorded at the Brooks Lake weather station. The clear conditions that prevailed and the high phytoplankton population doubtless provided a higher than average production there, but even at half the rate the trend of higher productivity toward the tributary end of the lake is maintained.

On 4 August parallel primary productivity measurements were made in the Iliuk arm (Station B) and the regular station (Station A) on Naknek Lake 3 mi to the west of Station B (Fig. 1). These measurements were to compare the primary productivity of the water at Station A with water nearer the mouths

of the Savonoski and Ukak Rivers. Because of the contribution of ash, pumice, and glacial outwash from these two streams, the Secchi depth at Station B was only 2.5 m as compared with 6.5 at the regular station. Although temperature recording equipment was inadequate for precision, thermometer values from the water samples at each depth above 10 m show an average increase of 1.8°F from Station B to Station A. Below 10 m the temperatures of the two stations were identical.

The rate of carbon fixation at different depths at Stations A and B in the two water columns is illustrated in Fig. 6. Although light inhibition at the surface was more the rule than the exception in Naknek Lake as well as in Brooks Lake, the measurements of 4 August were made under cloudy conditions. This is the probable explanation for the high photosynthetic rate at the surface, as there was not a significant difference in the plankton between the surface and one meter. The variability in productivity with depth reflects the heterogeneous distribution of phytoplankton which was evident from centrifuge and inverted microscope analyses of plankton in both Brooks and Naknek Lakes. The mean productivity for 13 m at Station A was 8.71 mgC/m³/day as compared to 6.10 mgC/m³/day at Station B. Station A is more productive than Station B at all depths, except between 4.0 and 6.5 m. The lower productivity of the water column at Station B is probably not the result of lower temperature, since Station B is cooler between 4.0 and 6.5 m than Station A and still has higher production between these depths. Lower temperatures tend, also, to reduce respiration more than they reduce the rate of photosynthesis (Spoehr 1926).

The rapid decline in photosynthesis below 7 m at Station B suggests that light limitations imposed by the higher turbidity are responsible.

A comparison of all routine water analyses during the summer shows little detectable difference among the stations (Table 5). Analyses for phosphorus and nitrogen were near their limits of detectability with values below 0.0008 ppm registering as 0. When all depths are included at Stations I and III, there is a trend towards higher phosphorus content as one proceeds from Station I to III. If, however, only the first 5 m are included in the comparison, the trend is reversed. Nitrite nitrogen is appreciably higher at Station IV than it is at the other Brooks stations. Silicon increases towards Station IV regardless of whether only the first 5 m or the entire water columns are considered.

A comparison of Naknek Stations A and B similarly show only small differences in the amounts of the elements measured. Station B, nearer the main tributaries gave slightly higher average silicon, phosphorous, and total hardness values with nitrogen and alkalinity slightly lower than at Station A. Phosphorous and nitrogen values are probably at or close to their extreme range of reliability. In respect to the amount of silicon, which is very likely the most reliable of the photocolometric determinations re-

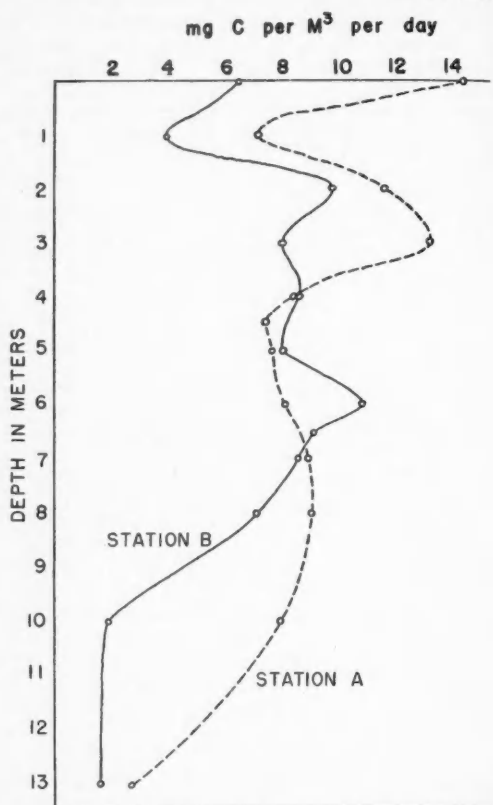


FIG. 6. Changes in photosynthetic rate with depth at Naknek Lake Stations B (solid line) and A (broken line), 4 August 1957.

TABLE 5. Water quality in three Alaskan Lakes, 1957. Values in ppm.

Lakes	BROOKS ¹				NAKNEK ²		BECHAROF ³
	I	II	III	IV	A	B	
Phosphorus.....	.0065	.0070	.00730087	.0095	.0083
Nitrite.....	.0015	.0012	.0019	.0038	.0083	.0050	.0030
Silicon.....	10.45	10.58	10.77	11.95	10.90	11.60	1.04
Total Hardness or ppm CaCO ₃ ...	36.13	35.17	35.48	69.50	71.0	24.90
Bound CO ₂ as ppm CaCO ₃	31.79	31.48	32.00	31.54	35.30	35.10	18.00

¹ Stations I, II, III, and IV, all comparative values July 4 to September 3, 1957.

² 4 August 1957. Mean of 0 and 13 m.

³ 23 August 1957. Mean of 0, 15, and 35 m.

ported here, it is of interest that the 13 m value (11.6 ppm) at Station A is the same as the mean value of the surface and 13 m at Station B. The surface value at A is lower (10.2 ppm). This difference might result from silica removal by diatoms in the surface layers, but more probably, since temperatures were the same below 10 m at the two stations, from the presence of the denser water mass from Station B close to the bottom at Station A.

The variation in productivity in Brooks and Naknek lakes from June to October is illustrated by the curves in Fig. 7. Both of these show very irregular seasonal decline in primary productivity from a high in June. If it were not for the comparison of Stations I and II, a histogram would be a better representation of these data (Rodhe *et al.* 1956). Diminishing light as the season progresses is generally recognized as a dominant factor at higher latitudes (Livingstone *et al.* 1958). Nutrient deficiencies may also contribute to a seasonal decline.

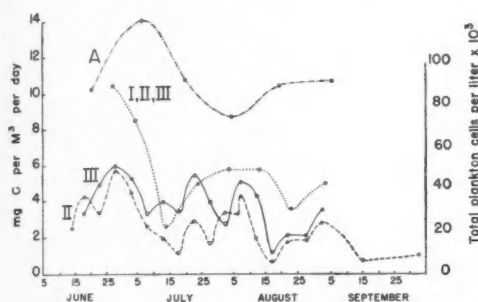


FIG. 7. Seasonal variation in photosynthesis at Brooks Lake Stations II (---) and III (—); and at Naknek Station A (·····). Also total phytoplankton at Brooks Stations I, II, and III (- · - · -).

Thermal stratification, although weak in comparison to more southerly latitudes, was evident by late June and remained until early September when there was evidence of mixing to 35 m. Temperatures in Naknek Lake were about two degrees warmer than in Brooks Lake during the summer, although daily variations were large in the shallower waters of both.

The seasonal change in the total phytoplankton of Brooks Lake (derived from the means of Stations I, II and III) is in rather good agreement with productivity measurements and lends support for a usable relationship between standing crop and rate of production estimates for major changes in productivity during a season (Fig. 7). Verduin (1956a) presents a formula for such estimates from standing crop measurements. Unfortunately, if nutrient or other factors are limiting, a crop built up before this deficiency may be producing very little additional organic matter at the time the estimate is made. In this situation standing crop measurements would give very unreliable values for the rate of production.

As might be expected at this northern latitude the dominating Phylum (Division) was the Chrysophyta. Its important genera were *Melosira*, *Stephanodiscus*, *Fragilaria*, *Asterionella*, *Tabellaria*, *Synedra*, and *Navicula*. The diatom population followed and was primarily responsible for the trimodal curve shown in Fig. 7. Next in abundance of both species and numbers were the Chlorophyta. The green algae were abundant in the samples taken in late June, and declined gradually throughout the rest of the summer except for a short lived increase at Stations III and

IV in early August. *Phacotus*, *Pediastrum*, *Ankistrodesmus*, and *Dictyosphaerium* were the most abundant genera. Of the Cyanophyta, *Microcystis* and *Lyngbya* were the only representatives evident throughout the summer. They formed a significant portion of the phytoplankton in the second half of August.

The total zooplankton population in Brooks Lake (measured at Stations I, II, and III) declined steadily throughout the season. The copepods were more abundant in the lake than cladocerans.

EXPERIMENTS ON NUTRIENT FACTORS LIMITING PRODUCTIVITY

The mere presence of chemical substances in the environment, although recognized as a valuable guide for pure culture studies (Provasoli & Pintner 1953), does not necessarily prove their biological availability (Potash 1956). Nevertheless because of the complexity of growth factors in natural waters (Hutchinson 1944), bioassay may be expected to reflect limiting factors better than chemical analysis of the environment.

As described under "Methods," culture series were run to identify the role of various nutrient factors in phytoplankton production in Brooks Lake during the summer portion of the red salmon growing season with three experiments in Naknek Lake and Lake Becharof for comparison. By starting Brooks Lake cultures at regular intervals, it was possible, further, to detect progressive seasonal changes in these limiting factors.

Although cultures were maintained for a sufficient time to allow significant population increases, the effect of specific nutrients on rate of carbon fixation was detectable (with C^{14} as a tracer) within a few minutes or hours after their addition to the media.

To demonstrate the efficiency of the method before field work was undertaken, a nitrogen deficient culture of *Scenedesmus quadricauda* Turp. was divided into two equal volumes. Five ppm of nitrogen was added as $Ca(NO_3)_2$ to one; the other was maintained as a control. Equal amounts of C^{14} were added to both. These were then subsampled four times during the 30-minute period immediately following the addition of $Ca(NO_3)_2$ and C^{14} . Fig. 8 illustrates the high sensitivity of this technique for measuring the increase in rate of photosynthesis initiated by the addition of $Ca(NO_3)_2$ to the nitrate deficient culture. Steemann Nielsen & Al Kholy (1956) have demonstrated that the C^{14} technique is applicable under conditions of phosphorus and nitrogen deficiency, although the discrepancy between the C^{14} and O_2 determination of photosynthesis is reduced by nitrogen and phosphorus addition (Ketchum *et al.* 1958). This is an important consideration since some of the measurements in the Alaskan lakes studied as well as in cultures were made under suboptimal concentrations of these two elements.

The first Brooks Lake culture experiment was started on 23 June and was maintained until 8 July. Of the variety of nutrients added, $MgSO_4$ was most

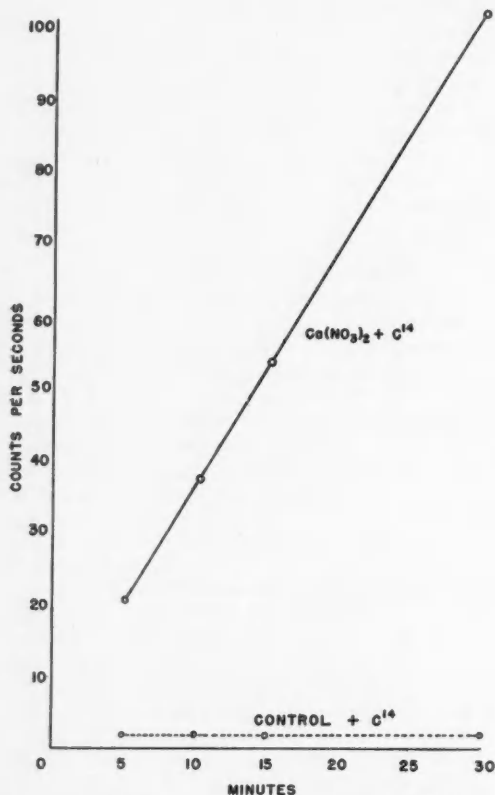


FIG. 8. C^{14} uptake with the addition of $\text{Ca}(\text{NO}_3)_2$ to a nitrogen deficient culture of *Scenedesmus quadricauda* Turp.

conspicuous as a stimulant to photosynthesis (Fig. 9). Although evident throughout the summer, the increase in the rate of carbon fixation stimulated by the addition of 9 ppm MgSO_4 was most pronounced in June. This corresponded to a high population of green algae (especially *Pediastrum* and *Ankistrodesmus*) and diatoms. That MgSO_4 was still in short supply in early July is indicated by a significantly higher production value in the culture of that month to which it had been added (Fig. 10). Similarly, the pure culture experiment started on the last day of July showed an appreciable gain upon the addition of this nutrient (Fig. 11).

In testing various concentrations of MgSO_4 with natural plankton populations, the quantity used initially, amounting to 9.0 ppm (1.82 ppm of Mg and 7.18 ppm of SO_4), was found to be about optimum. This concentration is within the range used by Rodhe (1948) to obtain optimum growth with *Ankistrodesmus falcatus* and is close to the quantity used by Potash (1956) in pond water with the green alga, *Kirchneriella subsolitaria* G. S. West, as an indicator organism.

Analysis by Beckman flame spectrophotometer of

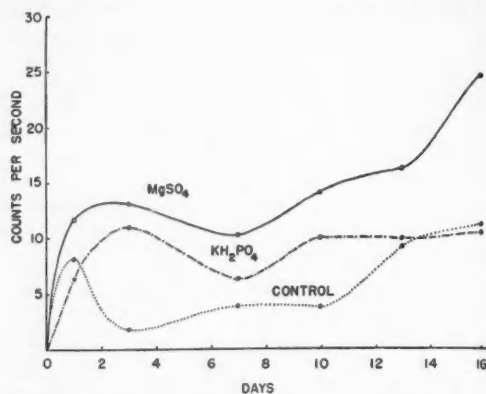


FIG. 9. Relative photosynthesis in phytoplankton cultures of Brooks Lake water to which MgSO_4 or KH_2PO_4 were added on 23 June 1957.

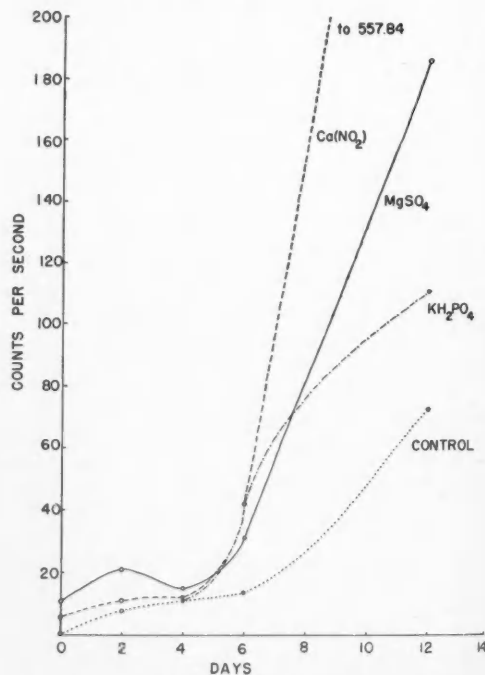


FIG. 10. Relative photosynthesis in phytoplankton cultures of Brooks Lake water to which MgSO_4 , $\text{Ca}(\text{NO}_3)_2$, or KH_2PO_4 were added on 6 July 1957.

Brooks Lake water collected in February 1958 indicated that 1.2 ppm of magnesium were present. Since the importance of magnesium as a limiting factor declined towards the end of the summer (Fig. 12) it is probable that lower magnesium levels or unfavorable cation ratios (Provasoli *et al.* 1954) existed in June and July. Turbidimetric determinations (American Public Health Association *et al.* 1955) gave 7.6 ppm sulfate. The addition of sulfate as CaSO_4 ,

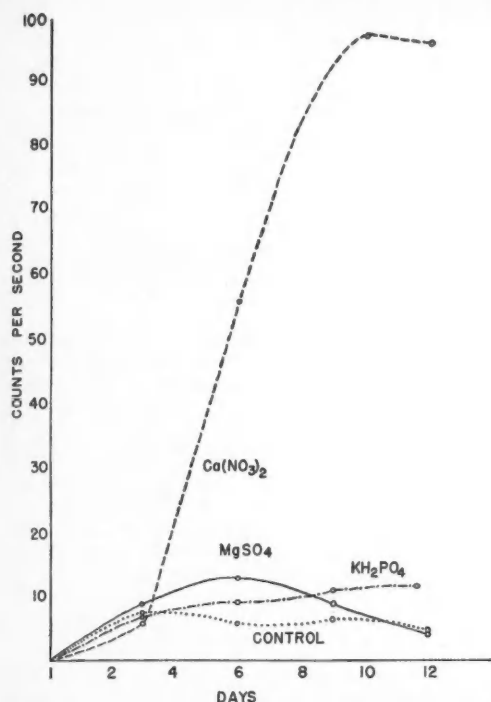


FIG. 11. Relative effect of nutrients on photosynthesis in pure cultures of *Ankistrodesmus falcatus* grown in Millipore filtered Brooks Lake water 31 July 1957.

Na_2SO_4 , and MnSO_4 in all possible combinations to water taken from Brooks Lake in February 1958 was stimulating to growth, but unless nitrate was provided, this stimulation was short lived.

To determine the relative importance of magnesium in different parts of the lake, surface water was collected at Stations I, III, and IV on 22 July. Each sample was subsequently divided into three 2-liter cultures. Because KH_2PO_4 and $\text{Ca}(\text{NO}_3)_2$ were also fairly consistent in initiating increases in the rate of carbon fixation above that of the control they were added together with Na_2CO_3 in two of the three cultures from each station. MgSO_4 was then added to one of these. The third was maintained as a control. A high rate of productivity in cultures was attained by the addition of MgSO_4 when other nutrients were not allowed to become limiting (Fig. 13). The deficiency of magnesium although evident at all stations decreases somewhat in the direction of the lake's main tributary.

The addition of MgSO_4 to a single culture of Naknek Lake water did not produce an increase in carbon fixation. With Lake Becharof water, however, MgSO_4 gave the highest rate of photosynthesis in the culture experiment conducted on 23 August.

To be certain that the addition of MgSO_4 or $\text{Na}_2\text{C}^{14}\text{O}_3$ to the cultures was not initiating the uptake of carbon by ion exchange mechanisms other than

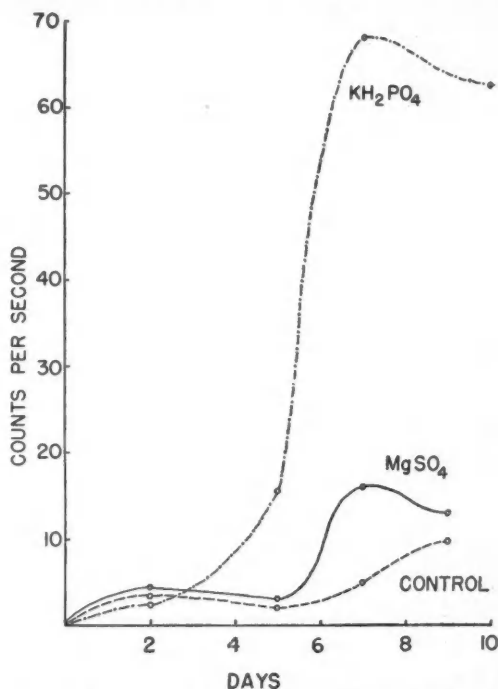


FIG. 12. Relative rates of photosynthesis in cultures of Brooks Lake phytoplankton to which MgSO_4 or KH_2PO_4 were added on 16 August 1957.

photosynthesis (e.g. by absorption into outer or apparent free space; Kramer 1957) an oxygen production experiment was run in addition to the regular maintenance of dark bottle controls with C^{14} experiments. Net O_2 production over a five-day period with 0.0, 2.5, and 5.0 microcuries of $\text{Na}_2\text{C}^{14}\text{O}_3$ added, was 0.72, 0.70, and 0.73 ppm of O_2 respectively. In a fourth sample 5.4 ppm of MgSO_4 produced 1.3 ppm of oxygen.

As a final check on the limiting nature of MgSO_4 in Brooks Lake, the same wire spreaders that were used for suspending duplicate samples for measuring experimental error in the regularly scheduled lake experiments were utilized to determine if there was a significant difference in C^{14} uptake between duplicate samples of lake phytoplankton at Station I. Because of the difficulty of assuming randomness even in dilute plankton populations, a non-parametric test (Wilcoxon Matched Pairs Signed Ranks Test; Siegel 1956) was utilized. The high efficiency (95%) with small samples made this test an excellent statistical treatment for these data.

When the Wilcoxon sum (10) was found to be well below the .05 level of significance (Table 6), the null hypothesis (H_0) was accepted and parallel samples were again taken. To one of each pair, 6 ppm of the nutrient being tested were added together with $\text{Na}_2\text{C}^{14}\text{O}_3$. The other, the control, was inoculated only with $\text{Na}_2\text{C}^{14}\text{O}_3$. These pairs were re-

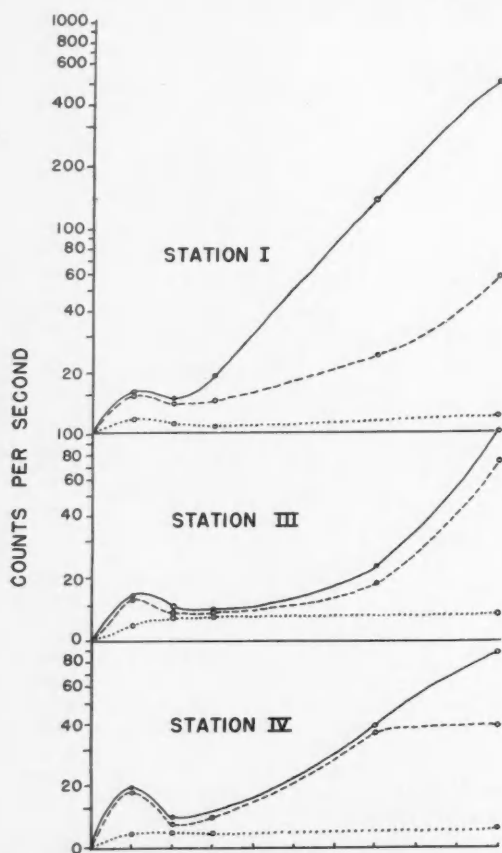


FIG. 13. Relative importance to photosynthesis of MgSO_4 in Brooks Lake cultures from Stations I, III, and IV. Solid line: MgSO_4 , $\text{Ca}(\text{NO}_3)_2$, KH_2PO_4 , and Na_2CO_3 added. Broken line: all of above nutrients added except MgSO_4 . Dotted line: control.

suspended at meter intervals from 0 to 5 m for 4 hrs of incubation; then their contents were filtered. This rapid bioassay technique had the advantage of measuring the immediate change in carbon fixation initiated by the addition of specific nutrients at a variety of depths without allowing time for population shifts, which, although not detected in the cultures, might conceivably have occurred in the nanoplankton.

TABLE 6. Relative rates of C^{14} assimilation (count/second) of algae from duplicate samples suspended at Station I. Decision: Accept H_0 .

Depth in meters	0	1	2	3	4	5
Sample A.....	2.21	1.68	1.11	3.26	2.01	1.80
Sample B.....	1.58	2.10	1.00	2.94	2.49	1.96

Carbon uptake increased at each depth of incubation in all samples to which 6 ppm of MgSO_4 had

been added. On a single end-test basis, the Wilcoxon sum of 0 is significant at the .025 level (Table 7).

TABLE 7. Relative rates of C^{14} assimilation (counts/second) of algae from samples of Brooks Lake water suspended at Station I with and without MgSO_4 added. Decision: Reject H_0 .

Depth in meters	0	1	2	3	4	5
Control.....	2.30	1.73	1.84	1.72	2.12	2.34
MgSO_4 added...	2.62	2.85	2.09	2.13	2.52	2.96

Calcium nitrate did not produce very significant increases in growth until July. In the culture started on 6 July (Fig. 10), the deficiency of this nutrient was not pronounced until the fourth day when the culture carrying an addition of $\text{Ca}(\text{NO}_3)_2$ began a rapid increase in rate of carbon assimilation. Twenty-five days later the lack of this nutrient in the lake water was even more pronounced as evidenced by the pure culture (Fig. 11) started on 31 July. The second major green algae pulse in the lake was evident at this time. The response to the addition of $\text{Ca}(\text{NO}_3)_2$ resembles the preliminary laboratory experiment with *Scenedesmus quadricauda* (Fig. 8).

Unfortunately the only nitrogen determinations that reagents were available for during the field season were for nitrite rather than the more stable and preferable nitrate. The relationship between ammonia, nitrate, and nitrite is apt to be unstable, although nitrate values are likely to be higher. The nitrite values are included in this study because they appear to show a relationship between the available nitrogen in the lake and results of culture experiments. The bioassay technique provides the best basis for assessing nitrogen deficiency.

It is of interest that in the single culture experiment in late August utilizing Naknek Lake water with its natural phytoplankton population, the only nutrient that significantly stimulated carbon assimilation above that of the control was $\text{Ca}(\text{NO}_3)_2$. At this time nitrite nitrogen values for the lake were appreciably higher than they were in Brooks Lake. The same experiment with Lake Becharof water on 15 July and 23 August showed only a slight photosynthetic increase in July by the addition of $\text{Ca}(\text{NO}_3)_2$, but in August the stimulating effect of this nutrient was very marked. Lake Becharof nitrite nitrogen for 23 August was at a level above the mean Brooks Lake determination for the same day.

Rodhe (1948), using *Ankistrodesmus falcatus*, found $\text{Ca}(\text{NO}_3)_2$ to be a better source of nitrogen for this organism than NH_4Cl and recommended 29.4 mg $\text{Ca}(\text{NO}_3)_2$ per liter as the lowest level for achieving optimum growth. Only 6.1 mg per liter were used in the Brooks Lake study.

In Brooks Lake water there was a decrease in nitrogen, measured as nitrite, during August and early September (Figure 14), concomitant with the deficiency noted in the pure culture experiment (Fig.

12). As already mentioned, in reference to the $MgSO_4$, Brooks Lake water collected in February and used in pure culture experiments in the laboratory gave elevated rates of production when nitrate was added in combination with any one of the following: calcium, magnesium, or sodium. Cultures of *Ankistrodesmus falcatus* to which the three foregoing cations were added individually soon turned from green to yellow with a decrease in rate of photosynthesis. When nitrate was added to these cultures they recovered. This clearly demonstrated that nitrogen was the deficient element.

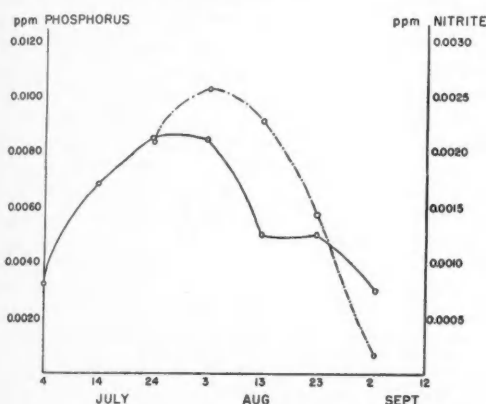


FIG. 14. Average seasonal variation (mean of 0 and 5 meters Station I) of nitrite nitrogen (solid line) and phosphorus (broken line) in Brooks Lake.

With the advent of a new limiting factor in the July cultures, it seemed advisable to repeat the experiment *in situ* at Station I. This time $Ca(NO_3)_2$ instead of $MgSO_4$ was added to one of each of the parallel samples (Table 8). Again utilizing the Wilcoxon Matched Pairs Signed Ranks Test, the increase in carbon assimilation initiated by the addition of $Ca(NO_3)_2$ gives a significant Wilcoxon sum of 1.0 (.05 level = 2.1, .025 level = 0).

TABLE 8. Relative rates of C^{14} assimilation (counts/second) of algae from samples of Brooks Lake water suspended at Station I with and without $Ca(NO_3)_2$ added. Decision: Reject H_0 .

Depth in meters	0	1	2	3	4	5
Control	5.11	7.24	7.17	4.46	3.11	3.47
$Ca(NO_3)_2$ added.	6.31	9.25	7.04	6.03	3.37	5.40

Phosphorus, as KH_2PO_4 , although a consistent stimulant to culture growth throughout the summer (Figs. 9, 10, and 11), did not increase the photosynthetic rate in the cultures to the extent that $MgSO_4$ and $Ca(NO_3)_2$ did until middle August (Fig. 12). This corresponded to a relatively high blue-green algae population. An environmental decline in phosphate is in close agreement with culture results.

Despite a very low potassium level of 0.94 ppm the addition of potassium as K_2SO_4 to pure cultures did not produce a significant photosynthetic increase.

In Lake Becharof, KH_2PO_4 was the most conspicuous stimulating nutrient in the July experiment. The August cultures of Lake Becharof water did not demonstrate this deficiency, and water analysis at this time showed phosphorus to be at a higher level than in Brooks or Naknek Lakes.

It is common knowledge to aquatic biologists that a large percentage of nutrient material, both organic and inorganic, is lost to the ecosystem by deposition as bottom sediment or by binding in aquatic plants (e.g. Hutchinson & Bowen 1950; Hayes *et al.* 1952). Under natural conditions no large-scale release of nutrients occurs unless the oxidized layer of the surface muds disappears (Mortimer 1949). Sedimentation, as in Danish fiords, can be assumed to take place at a faster rate than regeneration (Grøntved & Steemann Nielsen 1957). The recirculation of nutrients freed for reutilization in the system by decomposition is accomplished by eddy diffusion or by overturn in spring and fall. Mechanical agitation (Zieker *et al.* 1956), artificially turning over a lake (Hooper *et al.* 1953), or introduction of compressed air (Schmitz & Hasler 1958), has been suggested as a possible means of increasing the efficiency of the system.

While using SCUBA equipment to inspect the shelf area of Brooks Lake, the author noted that clouds of bottom sediment billowed up as he walked along the bottom. The extremely fine texture of the superficial bottom deposits suggests that mechanical resuspension might easily be achieved if it could be demonstrated that release of soluble nutrients in such bottom material would indeed be beneficial to the metabolism of the lake.

In Brooks Lake, analysis of sediment extract indicated that it contained .062 ppm of phosphorus compared to the lake's .0057 ppm. It also had .023 ppm of nitrite in contrast to the lake's .0012 ppm, and 6.0 ppm more SiO_2 than the lake water. Additions of 1% and 2% by volume of this extract to cultures of Brooks Lake water increased the rate of photosynthesis appreciably (Table 9).

TABLE 9. Assay with C^{14} of the nutrient contribution of bottom sediment extract to cultures of Brooks Lake phytoplankton, in counts/second.

Amount of extract added	DAYS				
	1	2	5	7	11
0% (Control)	3.63	6.50	5.81	2.56	3.47
1%	6.17	8.64	5.98	4.56	...
2%	9.17	10.28	9.60	6.84	5.32

DISCUSSION

The importance of lake basin morphometry in influencing lake productivity has received considerable attention since the pioneer work of Thienemann

(1927) and Naumann (1929). Because morphometry affects temperature, thermal and chemical stratification, and dilution and circulation of nutrients, mean depth, as the best indicator of morphometry, has been suggested as a dominant factor in productivity (Rawson, 1952). The extreme variability between lakes precluding any sharp delineation between types has, however, led Larkin & Northcote (1958) to conclude that only the total dissolved solid content could be used as an index of production in their studies.

The information gained from the Brooks Lake studies indicates that, if the productivity of the water alone is considered, the quantity and quality of replenished nutrients by the inflow of tributary streams is a much more important factor than depth. Important considerations in this respect, however, are the benthic development in the littoral zone which would certainly increase the productivity on a surface area basis and antimetabolites which might cause antagonistic interactions between plankton and sessile algae (Jorgensen 1956).

Traditionally the productivity per unit of surface area has been used for comparing different water bodies. On this basis, as in the comparison of Brooks and Naknek lakes, a long euphotic zone may compensate for a lower production per unit volume. There can be little doubt, however, that zooplankton or fish can feed at a faster rate if their food supply is concentrated. Richman (1958) has demonstrated an increase in net efficiency of young production (from 52.08 to 70.46%) by *Daphnia pulex* with increase in the concentration of food supply. Since the food levels he used were well above those encountered in Brooks Lake, higher phytoplankton densities may support a faster rate of zooplankton production. I would expect to find a significantly larger average size of red salmon migrating from Naknek Lake compared with those migrating from Brooks Lake. Supporting this speculation is the recent work (Nelson 1958) on the relationship between photosynthesis and growth of the juvenile red salmon in Bare Lake.

Eicher & Rounsefell (1957), working from fishery statistics, crude soil tests, chemical analyses of lake water, plankton production, and tree growth rings, have suggested that lake fertility may have been significantly increased in the lakes that received volcanic ash during the eruptions of 1912 and 1913. This is especially pertinent to the discussion because Brooks and Naknek Lakes were the only ones on the peninsula thought to have received the ash. Martin (1913) reported that the ash fall extended only as far west as Brooks Lake and the Iliuk arm of Naknek Lake. This reached a maximum thickness of 20 in., and, although covered by a thin layer of humus, is still clearly visible in the area when a shallow excavation is made.

Perhaps the greatest weakness in considering the pumice and ash as a nutrient source is evident from its chemical composition. Griggs (1920), who investigated the recovery of vegetation at Kodiak,

makes rather a strong argument of this. He points out the basic difference between this geologically fresh, acid ash and the lava of the Columbian region and further notes that the former has practically the same composition as pulverized granite. He goes on to state that the widespread idea that luxuriant growth of vegetation was due to some fertilizer in the ash was erroneous. Griggs attributes recovery of vegetation to mulching and reduced competition. Attempts at growing wheat in the ash failed, as death ensued as soon as the nutrients stored in the seed were exhausted.

Analysis of the ash compared with the composition of average igneous rock (Pettijohn 1957), showed the latter to be higher in almost every element except silicon. White pumice, hurled out by the eruption, was composed of rhyolitic magma with a silica content of 75%. The high concentration of this important element (Lund 1950) in Brooks and Naknek Lakes is in sharp contrast to Lake Becharof whose watershed did not receive the volcanic pumice or ash. The important water soluble salt potash (K_2O) was especially low in the ash and in Brooks Lake. Griggs (1919) also noted that rankest growth of *Calamagrostis langsfordii* occurred where evaporation was evidently concentrating the meager salts.

The greatest deficiency in the ash from the standpoint of plant growth, however, was nitrogen (Griggs *ibid.*). The first plant invader of the ash was the lupine (*Lupinus nootkatensis*) which has its own nitrogen-fixing bacteria. Shipley (1919a), chemist for the 1917 Katmai expedition, noted that the high ferrous sulfate content of the ash was not only directly injurious to plant growth, but also inhibited the action of nitrifying bacteria, thereby indirectly reducing the supply of an essential element.

The sub-optimal level of nitrogen in Brooks Lake evidenced by a number of culture experiments during July and August is of special interest since meteorological and geological evidence from the region are in good agreement with these findings. Although the primary source of nitrogen is from the atmosphere, Hutchinson (1957) concluded that in most lakes the origin of fixed nitrogen is to be found in the soils of the drainage basin. It is worth noting at this point that atmospheric nitrogen is not utilized by most algae as is ammonia or nitrate (Kratz & Myers 1955). Shipley (1919b), who was more than casually interested in the nitrogen problem in this area, made numerous determinations for the ammonia and the nitrous nitrogen in the rainwater of southwestern Alaska. Using Nessler's reagent, he found an almost entire absence of ammonia in the rainfall of this region in striking contrast to similar measurements made at about the same latitude in Europe. His highest value was 0.015 ppm NH_3 as compared with the lowest value observed in Scotland of 0.44 ppm. He found nitrate nitrogen in the rainfall along Shelikof Strait from August to September averaged only 0.0018 ppm and noted that nitrites were not transformed to nitrates.

Nitrogen fixation by algae (blue-green) has been recognized for some time (Fogg 1951, William & Burris 1952) and has been demonstrated to increase the yields of rice fields (Watanabe 1956). The lower phosphorus level in the lake in late August might reflect a higher requirement by nitrogen-fixing organisms. The carcasses of spawned-out salmon might also provide a significant amount of nitrogen and phosphorus if the escapement is of great size (Nelson & Edmondson 1955). Unfortunately most of this contribution comes at a time of rapidly declining light intensity and the normal nutrient recirculation by the fall overturn.

The nitrogen contribution of spring or melt water would appear negligible, as Shipley (1919b) commented that it was not necessary to prepare distilled water because of the almost total absence of either nitrous nitrogen or ammonia nitrogen in the spring and creek waters of the district as well as water obtained from melting snow. While the volcanic ash in question contains less than 1% of the nitrogen found in cultivated soil, the tundra of the region has a total nitrogen content of 43.0 ppm which is appreciably higher than Illinois prairie soils or the black loam of the Red River Valley, which Shipley (1919c) used for comparison. He associated this high nitrogen content with a low rate of nitrification in the cold, shallow tundra soil.

Another soil source of nitrogen which has received attention in recent years (Virtanen *et al.* 1955, Virtanen 1957) and which may have been a factor in Shipley's measurements is the alder shrub (*Alnus*). These plants are abundant in the area and have nitrogen-fixing bacteria in root nodules. Although some of the nitrogen leaks directly into the soil, most is deposited in the leaves, which, falling to the ground, add to the soil annually as much as 140 lbs of nitrogen per acre (Lawrence 1958). The possible contribution of alders to lake fertility is certainly worthy of further investigation.

From the above it would appear that the most important source of nitrogen in the area may be from such streams as Headwater Creek, which have their source in the tundra and alder thickets. This hypothesis finds support in the increase in productivity towards the tributary end of the lake as well as in the chemical analysis summarized in Table 5. On 22 July (after a 0.30 in. rain on 21 July) the nitrite nitrogen at Station IV was over twice the average at the other three Brooks stations measured the following day. Thus it would appear that rainfall soaking through the nitrogen rich tundra before entering tributary streams may be a significant factor in the lake fertility of the region. In Brooks Lake, as observed in the sea (Ketchum 1947, Steemann Nielsen 1958), the rate of replenishment of nutrients, rather than the concentration at any given time, determines the fertility of the environment.

Recently sulfate has been found to be a limiting factor in Lake Victoria, Africa (Fish 1955). Even without the chemical analyses and experimentation

by addition of sulfate in various forms, the geology of the Alaska Peninsula and analysis of the ash might well suggest a deficiency of magnesium rather than sulfate in this region. Average igneous rock contains almost 3.5% magnesia (MgO). The ash that blanketed the area discussed contained less than 0.5%.

One thing that the eruption certainly did contribute to the area was sulfate. Following the eruption, rain containing high concentrations of sulfuric acid fell over large areas of Alaska (Griggs 1917). As far away as Prince William Sound, 300 mi (483 km) to the east, concentrations were high enough to burn the flesh. Even before the eruption, however, Spurr (1898), in a reconnaissance in southwestern Alaska, noted precipitates of iron and sulfur in hot springs of the Katmai pass. Thawing has been noted in upper Naknek Lake (the Iliuk arm) with air temperatures of $15^{\circ}F$ ($-9.6^{\circ}C$). This was also considered indicative of hot springs by early explorers (Griggs 1922). Depth was perhaps more important.

Magnesium, occupying the center of the chlorophyll molecule, is essential for both plant growth and chlorophyll formation. Experimental increase of magnesium concentration in *Chlorella* cultures, even at levels which do not appreciably increase the chlorophyll content, results in an increase in photosynthetic rate (Hill & Whittingham 1955). Like potassium, magnesium has long been recognized as a necessity for life but has not been considered as a limiting factor for phytoplankton development in lakes (Rodhe 1948).

After converting the extensive ionic water analysis of Lohammar (1938) to percentages of equivalents, Rodhe (1949) found close agreement between these and his own analysis of Swedish lakes as well as with those of the world (Clarke 1924). Cations in Brooks Lake as determined by flame spectrophotometer were converted to percentages of equivalents for comparison with these figures (Table 10). This table illustrates a divergence from the usual concentrations in two respects. First the Ca/Mg ratio is much higher in Brooks Lake and secondly the magnesium-sodium relationship is reversed from the usual. The first is of interest in respect to the work by Provasoli *et al.* (1954) which indicates that below monovalent/divalent ratios of 1.3 the range of favorable Ca/Mg ratios for growth of *Synura* sp. is restricted. In contrast the above-mentioned workers found *Fragilaria capucina* does well below this level. The diatom predominance in Brooks Lake is therefore in accord with a monovalent/divalent ratio of 0.31. The second is of interest in relation to the culture work. Magnesium, demonstrated to be very stimulating to phytoplankton growth during much of the season, is less available for plants in the presence of increased quantities of sodium or potassium (Leeper 1952).

It would appear from the evidence at hand that although potassium uptake by cells is independent of the presence or the absence of sodium (Scott & Hayward 1954), the already low magnesium level in

TABLE 10. A comparison of cation percentages of equivalents.

Cation	Enture world (Clarke 1924)	Brooks Lake	Upland, 1-21 (Lohammar 1938)
Ca ⁺⁺	63.5	63.9	67.3
Mg ⁺⁺	17.4	12.7	16.9
Na ⁺	15.7	20.3	13.6
K ⁺	3.4	3.1	2.2

comparison to other cations is made less available in Brooks Lake by the presence of relatively higher quantities of sodium. The slightly higher levels of phosphorus and nitrogen evident early in the summer are therefore of limited use to the phytoplankton population. Uptake during this period may represent luxury consumption above the phytoplankton requirements (Gerloff & Skoog 1954). As the levels of nitrogen decline, the relative optimum levels of MgSO₄ may also be depressed to the actual level of the environment. This situation was observed in cultures of the fungus *Mucor hiemalis* by Fothergill (1954). He found that with lower NH₄NO₃ concentrations optimal growth was obtained at reduced levels of MgSO₄ and that K₂HPO₄ has little influence on this relationship.

Very little published data are available on primary productivity in arctic lakes. Those that are available are difficult to compare because of the variety of techniques used. Early studies were made by the oxygen method and were usually reported in terms of gross photosynthesis. This is the case in the measurements near Point Barrow, Alaska, by Comita & Edmondson (1953), and the measurements at Bare Lake before and during fertilization (Nelson & Edmondson 1955). The very limited freshwater work with C¹⁴ is listed by Lund & Talling (1957).

Before the completion of this study, however, Frey & Stahl (1958) made measurements of primary productivity with C¹⁴ on 13, 16, 19, and 20 August, 1957 in a pond and a lake on Southampton Island in the Canadian arctic. Although the two measurements in the lake (designated S-7) were made for periods of 20 and 24.5 hours, their daily estimates are of interest for comparison with measurements in Brooks, Naknek, and Becharof Lakes during the same period. After correcting their two measurements at S-7 to mgC/m³/day, it is obvious that the difference between the two was not of significant magnitude to necessitate the inclusion of both in the comparison they made with Imikpuk and Bare Lakes. Since the inorganic carbon used in their calculation was approximately half that present, a corrected figure appears in parentheses. The estimate for mgC/m³/day is 1.5 (2.9) in S-7, as compared with 1.96 in Brooks Lake on 22 August, 10.42 for Naknek Lake on 19 August, and .63 in Lake Becharof on 23 August. The alkalinity of S-7 was over twice that of the three lakes just compared. Since variations in Brooks Lake with seasonal and meteorological con-

ditions range from well below 1.96 to a maximum of 9.86, there is little point in carrying the comparison further than to note that these lakes were all converting solar energy at a rather low rate in comparison to other lakes of the world (Vollenweider 1956).

If the primary productivity in Brooks Lake continued to follow the light values downward after the last sampling date in October (a not unreasonable assumption), about half of the annual production was measured during the season. On this basis an estimate of productivity for Brooks Lake is about twice that of the Sargasso which Steemann Nielsen & Jensen (1957) estimate at 1 mgC/m³/day, or 50 mgC/m²/day.

Problems in connection with fertilization have been covered by a number of authors (*e.g.* Hutchinson & Bowen 1950, Hasler & Einsele 1948). The experiments reported here provide a feasible approach to the establishment of a rationale for increasing basic productivity, and the C¹⁴ technique as adapted in these studies provides the fastest and most sensitive means yet devised for assessing nutrient limiting factors in natural waters. The Brooks Lake shelf areas hold a great store of nutrients that might be released by mechanical agitation. Since light is frequently inhibiting in very shallow water the increase in turbidity might be more beneficial than detrimental. If fertilization is to be tried in a lake on a trial basis, it should be done with due respect to the factors actually limiting productivity, and should be balanced so as to supplement, not replace, the contribution of the watershed. The work reported here demonstrates the seasonal variation in these factors as well as marked differences in lakes of the same region. A careful investigation of the plankton nutrient requirements, seasonal changes in these requirements, and the trophic relationships of the consumers in individual lakes is of great importance in future work of this kind.

SUMMARY

1. The C¹⁴ technique was utilized for both bioassay of nutrient limiting factors and direct measurement of primary productivity in Brooks, Naknek, and Becharof Lakes. The efficiency of counting radioactivity was based on conversion of plankton to CO₂, thereby eliminating problems of geometry and self-absorption.

2. Comparisons of daily photosynthetic rate in Naknek and Brooks Lakes on a unit volume basis indicate a threefold higher rate in the former.

3. When photosynthetic rate is compared on a surface area basis, the difference is small.

4. The euphotic zone in Brooks Lake varied from about 25 m to over 50 m with an average for the season of 46 m.

5. The average primary productivity of Brooks Lake was higher on bright days than it was on cloudy days. The reverse was frequently the case in shallow water where light inhibition was especially evident.

6. The depth of the euphotic zone in Naknek

averaged about 16 m with considerable variation with changes in light and turbidity.

7. The possible relationships of Secchi depth to the euphotic zone are discussed with emphasis on the approximate nature of such comparisons.

8. Comparisons of the four Brooks Lake stations indicate that primary productivity per unit volume at comparable depths consistently increases towards the tributary end of the lake.

9. Comparisons of the primary productivity of Naknek Lake Stations A and B indicate a higher rate at the less turbid Station A.

10. Primary productivity measurements in Brooks Lake compare favorably with variations in total phytoplankton. Phytoplankton and zooplankton abundance both followed the seasonal decline in light energy so evident at these northern latitudes.

11. The sensitivity of the C^{14} technique was demonstrated in the laboratory with a nitrate deficient culture of *Scenedesmus quadricauda*.

12. Magnesium was found to be a limiting factor for phytoplankton production throughout the summer by both culture and *in situ* lake experiments. The relative importance of magnesium decreases somewhat towards the major tributary and also as other nutrients become limiting.

13. Magnesium deficiency was also noted in Lake Becharof in late August.

14. Nitrate deficiency was evident in Brooks Lake cultures in July and August. Results were verified in experiments *in situ*.

15. The single culture experiment in Naknek Lake indicated nitrate deficiency in late August. The Lake Becharof experimental cultures in July showed only slight stimulation with the addition of nitrate; in the August culture, the nitrate addition was considerably more stimulating.

16. Phosphorus, although consistently stimulating to photosynthesis, did not appear as critical as $MgSO_4$ or $Ca(NO_3)_2$ until middle August. An environmental decline was observed at this time. In Lake Becharof, although phosphorus was of primary importance in July, by August environmental levels were above those in Brooks and Naknek Lakes and the cultures derived no measurable benefit from its addition.

17. Brooks Lake bottom sediment extract was very stimulating to cultures of the natural phytoplankton population.

18. A discussion is given on published work related to the problems of primary productivity and fertility in arctic lakes.

LITERATURE CITED

- Åberg, B. & W. Rodhe. 1942. Über die Milieufaktoren in einigen südschwedischen Seen. *Symb. Bot. Ups.* 5: 1-256.
- Akehurst, S. C. 1931. Observations on pond life, with special reference to the possible causation of swarming of phytoplankton. *Jour. Roy. Micros. Soc.* 51: 237-265.
- American Public Health Association et al. 1955. Standard methods for the examination of water, sewage and industrial wastes. 10th Ed. New York: American Public Health Association. 522 pp.
- Arkin, H. & R. R. Colton. 1953. Statistical methods. New York: Barnes and Noble, Inc. 4th Ed. 224 pp.
- Atkins, W. R. G. 1922. Hydrogen-ion concentration of sea water in its biological relation. *Jour. Mar. Biol. Assoc. U. K.* 12: 717.
- . 1923. Phosphate content of waters in relation to growth of algal plankton. *Jour. Mar. Biol. Assoc. U. K.* 13: 119-150.
- Atwood, W. W. 1911. Geology and mineral resources of parts of the Alaskan Peninsula. *U. S. Geol. Surv. Bull.* 467. 137 pp.
- Barnaby, J. T. 1944. Fluctuations in abundance of red salmon, *Oncorhynchus nerka* (Walbaum), of the Karluk River, Alaska. *U. S. Fish and Wildlife Serv., Fish. Bull.* 39(50): 237-295.
- Bernstein, W. & R. Ballentine. 1950. Gas phase counting of low energy Beta-emitters. *Rev. Sci. Instruments* 21: 158-162.
- Chu, S. P. 1942. The influence of the mineral composition of the medium on the growth of planktonic algae. I. Methods and culture media. *Jour. Ecol.* 30: 284-325.
- Clarke, F. W. 1924. The data of geochemistry. *U. S. Geol. Surv. Bull.* 770. 5th Ed. 841 pp.
- Clarke, G. L. 1954. Elements of ecology. New York: J. C. Wiley & Sons. 534 pp.
- Comita, G. W. & W. T. Edmondson. 1953. Some aspects of the limnology of an arctic lake. *Stanford Univ. Pubs. Biol. Sci.* 11: 7-13.
- Doty, M. S. & M. Oguri. 1957. Evidence for a photosynthetic daily periodicity. *Limnol. and Oceanogr.* 2(1): 37-40.
- Dussart, B. 1950. La productivité de l'eau de mer. *Conf. Cent. Rech. Etud. Oceanogr.* 6. 6 pp.
- Edmondson, W. T. 1956. The relation of photosynthesis by phytoplankton to light in lakes. *Ecology* 37: 161-174.
- Edmondson, W. T. & Y. H. Edmondson. 1947. Measurements of production in fertilized salt water. *Jour. Mar. Res.* 6: 228-246.
- Eicher, G. J. & G. A. Rounsefell. 1957. Effects of lake fertilization by volcanic activity on abundance of salmon. *Limnol. and Oceanogr.* 2: 70-76.
- Fenner, C. N. 1923. The origin and mode of emplacement of the Great Tuff Deposit of the Valley of Ten Thousand Smokes. *Tech. Pap. Nat. Geogr. Soc., Katmai Ser.* 1. 74 pp.
- Fish, G. R. 1955. Chemical factors limiting growth of phytoplankton in Lake Victoria. *Jour. E. African Agric.* 21: 152-158.
- Foerster, R. E. 1944. The relation of lake population density to size of young sockeye salmon (*Oncorhynchus nerka*). *Jour. Fish. Res. Bd. Canada* 6: 267-280.
- . 1954. On the relation of adult sockeye salmon returns to known smolt seaward migrations. *Jour. Fish. Res. Bd. Canada* 11: 339-350.
- Fogg, G. E. 1951. Nitrogen fixation by *Mastigocaulus laminosus* Cohn. *Jour. Expt. Bot.* 2: 117-120.
- Forbes, S. A. 1887. The lake as a microcosm. Republished in 1925. *Ill. Nat. Hist. Surv. Bull.* 15: 537-550.
- Fothergill, P. G. 1954. The mineral nutritional re-

- quirements of *Mucor hiemalis*. Jour. Gen. Microbiol. 10: 17-26.
- Frey, D. G. & J. B. Stahl. 1958. Measurements of primary production on Southampton Island in the Canadian Arctic. Limnol. and Oceanogr. 3: 215-221.
- Gaarder, T. & H. H. Gran. 1927. Investigations of the production of plankton in the Oslo Fjord. Jour. Cons. Internatl. Explor. Mer 42: 1-48.
- Gardener, A. C. 1943. Measurement of phytoplankton population by the pigment extraction method. Jour. Mar. Biol. Assoc. U. K. 25: 739-744.
- Gerloff, G. C. & F. Skoog. 1954. Cell contents of nitrogen and phosphorus as a measure of their availability for growth of *Microcystis aeruginosa*. Ecology 35: 348-353.
- Gessner, F. 1949. Der Chlorophyllgehalt im See und seine photosynthetische Valenz als geophysikalische Problem. Schweiz. Ztschr. Hydrol. 11: 378-410.
- Goetz, A. & N. Tsuneishi. 1951. The application of molecular filter membranes to the bacteriological analysis of water. Jour. Amer. Waterworks Assoc. 43: 943-969.
- Goldberg, E. D., M. Baker & D. L. Fox. 1952. Microfiltration in oceanographic research. I. Marine sampling with the molecular filter. Jour. Mar. Res. 11: 194-204.
- Grøntved, J. & E. Steemann Nielsen. 1957. Meddelelser fra Kommissionen for Danmarks Fiskeriog Havundersøgelse. Serie: Plankton. Bind 5. 52 pp.
- Griggs, R. F. 1917. IV. The character of the eruption as indicated by its effects on vegetation. Ohio Jour. Sci. 19(3): 173-209.
- . 1919. IX. The beginning of revegetation in Katmai Valley. Ohio Jour. Sci. 19: 318-342.
- . 1920. The recovery of vegetation at Kodiak. Ohio State Univ. Bull. 24(15): 1-57.
- . 1922. The Valley of Ten Thousand Smokes. Washington: The National Geographic Society. 341 pp.
- Hasler, A. D. & W. G. Einsele. 1948. Fertilization for increasing productivity of natural inland waters. Trans. N. Amer. Wildlife Conf. 13: 527-555.
- Hayes, F. R., J. A. McCarther, M. L. Cameron & D. A. Livingstone. 1952. On the kinetics of phosphorus exchange in lakes. Jour. Ecol. 40: 202-216.
- Hill, R. & C. P. Whittingham. 1955. Photosynthesis. London: Methuen and Co., Ltd. 165 pp.
- Hooper, F. F., R. C. Ball & H. A. Tanner. 1953. An experiment in the artificial circulation of a small Michigan lake. Trans. Amer. Fish. Soc. 82(1952): 222-241.
- Hutchinson, G. E. 1944. Limnological studies in Connecticut. VII. A critical examination of the supposed relationship between phytoplankton periodicity and chemical changes in lake water. Ecology 25: 3-26.
- . 1957. A treatise on limnology. Vol. I. New York: J. C. Wiley & Sons. 1015 pp.
- Hutchinson, G. E. & V. T. Bowen. 1950. Limnological studies in Connecticut. IX. A quantitative radiochemical study of the phosphorus cycle in Linsley Pond. Ecology 31: 194-203.
- Ivlev, V. S. 1945. The biological productivity of waters. (In Russian, Preliminary Translation by W. E. Ricker) Adv. Mod. Biol., Moscow 19: 98-120.
- Jenkin, P. M. 1937. Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation to submarine illumination in the English Channel. Jour. Mar. Biol. Assoc. U. K. 22: 301-342.
- Jorgensen, E. G. 1956. Growth inhibiting substances formed by algae. Physiol. Plant. 9: 712-726.
- Ketchum, B. H. 1947. The biochemical relations between marine organisms and their environment. Ecol. Monog. 17: 309-315.
- Ketchum, R. H., J. H. Ryther, C. S. Yentsch & N. Corwin. 1958. Productivity in relation to nutrients. Cons. Internatl. Explor. de la Mer, Rapp. et Proc.-Verb. 144: 132-140.
- Kramer, P. J. 1957. Outer space in plants. Science 125(3249): 633-635.
- Kratz, W. A. & J. Myers. 1955. Nutrition and growth of several blue-green algae. Amer. Jour. Bot. 42: 282-287.
- Kuznetsov, S. I. 1956. Application of radioactive isotopes to the study of processes of photosynthesis and chemosynthesis in lakes. Proc. Internatl. Conf. Peaceful Uses of Atomic Energy. 12: Radioactive Isotopes and Ionizing Radiations in Agriculture, Physiology, and Biochemistry. pp. 368-376.
- Lapp, R. E. & H. L. Andrews. 1955. Nuclear radiation physics. New York: Prentice-Hall. 532 pp.
- Larkin, P. A. & T. G. Northcote. 1958. Factors in lake typology in British Columbia, Canada. Verh. Int. Ver. Limnol. 13: 252-263.
- Lasker, R. & R. W. Holmes. 1957. Variability in retention of marine phytoplankton by membrane filters. Nature 180: 1295-1296.
- Lawrence, D. B. 1958. Glaciers and vegetation in Southeastern Alaska. Amer. Scient. 46(2): 89-122.
- Leeper, G. W. 1952. Factors affecting availability of inorganic nutrients in soils with special reference to micronutrient metals. Ann. Rev. de Plant Physiol. 3: 1-15.
- Lefèvre, M., M. Nisbet & E. Jakob. 1949. Actions des substances excretées en culture, par certaines espèces d'Algues sur le métabolisme d'autres espèces d'Algues. Verh. Int. Ver. Limnol. 10: 259-264.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23: 399-418.
- Livingstone, D. A., K. Bryan, Jr. & R. G. Leahy. 1958. Effects of an Arctic environment on the origin and development of freshwater lakes. Limnol. and Oceanogr. 3: 192-214.
- Lohammar, G. 1938. Wasserchemie und höhere Vegetation schwedischer Seen. Symb. Bot. Ups. 3: 1-252.
- Lund, J. W. G. & J. F. Talling. 1957. Botanical limnological methods with special reference to the algae. Bot. Rev. 23: 489-583.
- Lund, J. W. G. 1950. Studies on *Asterionella formosa* Hass. II. Nutrient depletion and the spring maximum. Jour. Ecol. 38: 1-35.
- MacFadyen, A. 1948. The meaning of productivity in biological systems. Jour. Anim. Ecol. 17: 75-80.
- Manning, W. M. & R. E. Juday. 1941. The chlorophyll content and productivity of some lakes in northeastern Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 33: 363-393.
- Martin, G. C. 1913. The recent eruption of Katmai volcano in Alaska. Nat. Geogr. Mag. 24: 131-181.
- Mortimer, C. H. 1949. Seasonal changes in chemical

- conditions near the mud surface in two lakes of the English Lake District. *Verh. Int. Ver. Limnol.* 10: 353-356.
- Naumann, E. 1925. Handbuch der biologischen Arbeitsmethoden. Abt. IX, Methoden zur Erforschung der Leistungen des tierischen Organismus, Teil 2, 1. Hälfte, Heft 3: 543-652.
- . 1929. Einige neue Gesichtspunkte zur Systematik der Gewassertypen, mit besonderer Berücksichtigung der Seetypen. *Arch. f. Hydrobiol.* 20: 191-198.
- Nelson, P. R. 1958. Relationship between rate of photosynthesis and growth of juvenile red salmon. *Science* 128(3317): 205-206.
- Nelson, P. R. & W. T. Edmondson. 1955. Limnological effects of fertilizing Bare Lake, Alaska. *U. S. Fish and Wildlife Serv., Fish. Bull.* 56(102): 415-436.
- Nygaard, G. 1955. On the productivity of five Danish waters. *Verh. Int. Ver. Limnol.* 12: 123-133.
- Odum, H. T. & E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monog.* 25: 291-320.
- Ohle, W. 1956. Bioactivity, production, and energy utilization of lakes. *Limnol. and Oceanogr.* 1: 139-149.
- Olson, F. C. W. 1949. A system of morphometry. Tallahassee, The Oceanographic Institute, Florida State University. Contrib. 21. 20 pp.
- Perfiliev, B. W. 1929. Zur Mikrobiologie der Bodena-blagerungen. *Verh. Int. Ver. Limnol.* 4: 107-143.
- Pettijohn, F. J. 1957. Sedimentary rocks. New York: Harper Bros. 718 pp.
- Poole, H. H. & W. R. G. Atkins. 1929. Photo-electric measurements of submarine illumination throughout the year. *Jour. Mar. Biol. Assoc. U. K.* 16: 297-324.
- Potash, M. 1956. A biological test for determining the potential productivity of water. *Ecology* 37: 631-639.
- Pratt, R. 1943. Studies on *Chlorella vulgaris*. VI. Retardation of photosynthesis by a growth-inhibiting substance from *Chlorella vulgaris*. *Amer. Jour. Bot.*, 30: 32-33.
- Proctor, V. W. 1957. Studies of algal antibiosis using *Haematococcus* and *Chlamydomonas*. *Limnol. and Oceanogr.* 2: 125-139.
- Provasoli, L. & I. J. Pinter. 1953. Ecological implications of *in vitro* nutritional requirements of algal flagellates. *Ann. N. Y. Acad. Sci.* 56: 839-851.
- Provasoli, L., J. J. McLaughlin & M. R. Droop. 1957. The development of artificial media for marine algae. *Arch. f. Mikrobiol.* 25: 392-428.
- Provasoli, L., J. J. A. McLaughlin & I. J. Pinter. 1954. Relative and limiting concentrations of major mineral constituents for the growth of algal flagellates. *Trans. N. Y. Acad. Sci. (Ser. 2)* 16: 412-417.
- Pütter, A. 1924. Der umfang der Kohlensäurerreduktion durch die Planktonalgen. *Pflügers Arch. f. die Gesam. Physiol.* 205: 293-312.
- Rawson, D. W. 1952. Mean depth and the fish production of large lakes. *Ecology* 33: 513-521.
- Rice, T. R. 1954. Biotic influences affecting population growth of planktonic algae. *U. S. Fish and Wildlife Serv., Fish. Bull.* 54(87): 227-254.
- Richman, S. 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monog.* 28: 273-291.
- Ricker, W. E. 1937. The food and the food supply of sockeye salmon (*Oncorhynchus nerka*, [Walbaum]) in Cultus Lake, British Columbia. *Jour. Biol. Bd. Canada* 3: 450-468.
- Riley, G. A. 1940. Limnological studies in Connecticut. Part III. The plankton of Linsley Pond. *Ecol. Monog.* 10: 279-306.
- . 1941. Plankton studies, III. Long Island Sound. *Bingham Oceanogr. Coll. Bull.* 7: 1-93.
- Rodhe, W. 1948. Environmental requirements of freshwater plankton algae. *Symb. Bot. Ups.* 10: 149 pp.
- . 1949. The ionic composition of lake waters. *Verh. Int. Ver. Limnol.* 10: 377-386.
- Rodhe, W., R. A. Vollenweider & A. Nauwerck. 1956. The primary production and standing crop of phytoplankton. In: Symposium on perspectives in marine biology. Scripps Inst. Oceanogr. University of California Press. pp. 299-322.
- Ruttner, F. 1952. Planktonstudien der Deutschen Limnologischen Sunda-Expedition. *Arch. f. Hydrobiol., Suppl.* 21. 274 pp.
- Ryther, J. H. 1956. The measurement of primary production. *Limnol. and Oceanogr.* 1: 72-84.
- Ryther, J. H. & C. S. Yentsch. 1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. *Limnol. and Oceanogr.* 2: 281-286.
- Schmitz, W. R. & A. D. Hasler. 1958. Artificially induced circulation of lakes by means of compressed air. *Science* 128(3331): 1088-1089.
- Schmer, H. A. & C. Juday. 1933. Photosynthesis of algae at different depths in some lakes of northeastern Wisconsin. *Trans. Wis. Acad. Sci. Arts Lett.* 29: 173-193.
- Schreiber, W. 1927. Der Reinkultur von marinem phytoplankton und deren Bedeutung für die Erforschung der Produktionsfähigkeit des Meerwassers. *Wiss. Meeresuntersuch.* 16: 1-34.
- Scott, G. T. & H. R. Hayward. 1954. Evidence for the presence of separate mechanisms regulating potassium and sodium distribution in *Ulva lactuca*. *Jour. Gen. Physiol.* 37: 601-620.
- Serfling, R. E. 1949. Quantitative estimation of plankton from small samples of Sedgwick-Rafter cell mounts of concentrate samples. *Amer. Micros. Soc. Trans.* 68: 185-199.
- Shelford, V. E. 1913. Animal communities in temperate America. Chicago: University of Chicago Press. 362 pp.
- Shipley, J. W. 1919a. The water soluble salt content, the ferrous iron content and the acidity of volcanic ash. *Ohio Jour. Sci.* 19: 224-229.
- . 1919b. Ammonia and nitrous nitrogen in the rain water of southwestern Alaska. *Ohio Jour. Sci.* 19: 230-234.
- . 1919c. The nitrogen content of volcanic ash in the Katmai eruption of 1912. *Ohio Jour. Sci.* 19: 213-223.
- Siegel, S. 1956. Nonparametric statistics. New York: McGraw-Hill Book Co. 312 pp.
- Spoeher, H. A. 1926. Photosynthesis. New York: New York Chemical Catalogue Co., Inc. 393 pp.
- Spurr, J. E. 1898. A reconnaissance in S. W. Alaska. *U. S. Geol. Surv. Ann. Rep.* 20. 146 pp.

- Steemann Nielsen, E. 1951. Measurement of the production of organic matter in the sea by means of carbon 14. *Nature* 167: 684-685.
- . 1952. The use of radioactive carbon (C^{14}) for measuring organic production in the sea. *Jour. Cons. Internatl. Explor. Mer* 18: 117-140.
- . 1955. The production of antibiotics by plankton algae and its effect upon bacterial activities in the sea. *Pap. Mar. Biol. Oceanogr.*, Suppl. to Vol. 3 of *Deep-Sea Res.*, pp. 281-286.
- . 1958. The balance between phytoplankton and zooplankton in the sea. *Jour. Cons. Internatl. Explor. Mer* 23: 178-188.
- Steemann Nielsen, E. & A. A. Al Kholy. 1956. Use of C^{14} -Technique in measuring photosynthesis of phosphorus to nitrogen deficient algae. *Physiol. Plant.* 9: 144-153.
- Steemann Nielsen, E. & E. A. Jensen. 1957. Primary oceanic production. *Galathea Rep.* 1: 49-136.
- Strickland, J. D. H. 1958. Solar radiation penetrating the ocean. A review of requirements, data and methods of measurement, with particular reference to photosynthetic productivity. *Jour. Fish. Res. Bd. Canada* 15: 453-493.
- Strøm, K. M. 1933. Nutrition of algae. Experiments upon: the feasibility of the Schreiber method in fresh waters; the relative importance of iron and manganese in nutritive medium; the nutritive substances given off by lake bottom muds. *Arch. f. Hydrobiol.* 25: 38-47.
- Sverdrup, H. U., M. W. Johnson & R. H. Fleming. 1942. *The oceans. Their physics, chemistry, and general biology.* Englewood Cliffs, N. J.: Prentice-Hall, Inc. 1087 pp.
- Talling, J. F. 1957. The phytoplankton population as a compound photosynthetic system. *New Phytol.* 56: 133-149.
- Thienemann, A. 1927. Der Bau des Seebeckens in seiner Bedeutung für den Ablauf des Lebens im See. *Verh. Zool.-Bot. Ges. Wien* 77: 87-91.
- . 1931. Der produktionsbegriff in der Biologie. *Arch. f. Hydrobiol.* 22: 616-622.
- United States Department of Commerce Weather Bureau. 1957. Local climatological data with comparative data. Alaska, King Salmon. 4 pp.
- Van Slyke, D. & J. Folch. 1940. Manometric carbon determinations. *Jour. Biol. Chem.* 136: 509-541.
- Verduin, J. 1956a. Energy fixation and utilization by natural communities in western Lake Erie. *Ecology* 37: 40-50.
- . 1956b. Primary production in lakes. *Limnol. and Oceanogr.* 1: 85-91.
- . 1957. Daytime variations in phytoplankton photosynthesis. *Limnol. and Oceanogr.* 2: 333-336.
- Vinberg, G. G. & L. I. Iarovitsina. 1939. Daily changes in the quantity of dissolved oxygen as a method for measuring the value of primary production. *Trud. Limnol. Stantsii Kosine* 22: 128-143.
- Virtanen, A. I. 1957. Investigations on nitrogen fixation by the alder. II. Associated culture of spruce and inoculated alder without combined nitrogen. *Physiol. Plant.* 10: 164-169.
- Virtanen, A. I., T. Moisio, R. M. Allison & R. H. Burris. 1955. Fixation of nitrogen by excised nodules of the alder. *Acta Chem. Scand.* 9: 184-186.
- Vollenweider, R. A. 1956. Das Strahlungsklima des Lago Maggiore und seine Bedeutung für die Photosynthese des Phytoplanktons. *Mem. Ist. Ital. Idrobiol. de Marchi* 9: 293-362.
- Watanabe, A. 1956. On the effect of the atmospheric nitrogen-fixing blue-green algae on the yield of rice. *Bot. Mag. (Tokyo)* 69: 530-535.
- Williams, A. E. & R. H. Burris. 1952. Nitrogen fixation by blue-green algae and their nitrogenous composition. *Amer. Jour. Bot.* 39: 340-342.
- Yentsch, C. S. & J. H. Ryther. 1957. Short-term variations in phytoplankton chlorophyll and their significance. *Limnol. and Oceanogr.* 2: 140-142.
- Zicker, E. L., K. C. Berger & A. D. Hasler. 1956. Phosphorus release from bog lake muds. *Limnol. and Oceanogr.* 1: 296-303.

apha
No. 2
ogie.

reau.
ative

de-

a by
logy

nnol.

ktion
66.

nges
for
rud.

fixa-
ruce
gen.

arris.
the

des
hoto-
biol.

heric
rice.

fixa-
com-

aria-
gnifi-

1956.
and